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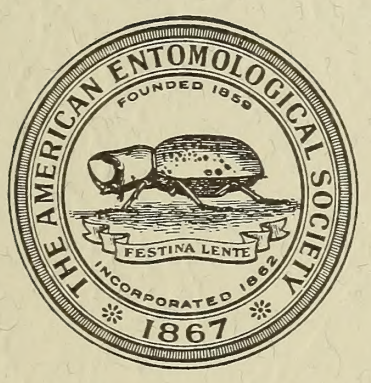
NUMBER 43

A WORLD REVISION OF THE GENUS *SPODOPTERA* GUENÉE (LEPIDOPTERA: NOCTUIDAE)

By

Michael G. Pogue



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A World Revision of the Genus *Spodoptera* Guenée (Lepidoptera: Noctuidae)

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ABSTRACT—The world fauna of the armyworm genus *Spodoptera* Guenée is revised. A phylogeny of *Spodoptera* was constructed based on cladistic relationships of the 30 species. Two genera that are sister groups of *Spodoptera* based on a molecular phylogeny of the Noctuidae served as outgroups. The data set contained 24 morphological characters (6 binary and 18 multistate) comprised of 134 character states. Cladistic analysis used the parsimony program Hennig86 which constructed two trees with a length of 143, a consistency index of 0.77, and a retention index of 0.91. Eight monophyletic clades containing 2 to 5 species were recognized. Two species were not part of any of the eight clades, but were sister taxa to larger monophyletic groups on the tree. These were *S. exigua* (Hübner) which was the most plesiomorphic species and *S. frugiperda* (J.E. Smith) was the sister species to the *dolichos, littoralis, evanida,* and *praefica* clades. Descriptions, distributions, and illustrations of all adults are included. Twenty species of larvae are described and 17 are illustrated. Keys are provided to adults based on geographical distribution, external morphology, and male and female genitalia. A key to larvae is based on color pattern and morphology. Ten neotypes and 32 lectotypes are designated and 5 new synonyms are proposed. Specimens examined during this study were given a bar code label. Databases of the bar coded specimens and all unique localities encountered during this study were developed. Databases were produced for larval host plants, parasitoids, predators, and a bibliography to the records contained in these databases. Databases can be found on the internet at the Systematic Entomology Laboratory and the Department of Entomology, Smithsonian Institution websites.

INTRODUCTION

Some of the most serious economic armyworm pests are species in the genus *Spodoptera* Guenée. Species are polyphagous on numerous vegetables, grain crops, and pasture lands. The genus is mainly tropical and subtropical throughout the world with some species migrating into more temperate regions throughout the growing season, e.g., *Spodoptera exigua* (Hübner) and *S. littoralis* (Boisduval) have been collected in northwestern Europe (Mikkola & Salmensuu 1965, Goater 1983). In the Western Hemisphere those species that are found in the temperate regions of the United States include *S. exigua, S. frugiperda* (J. E. Smith), *S. ornithogalli* (Guenée), *S. praefica* (Grote), *S. eridania* (Walker), and *S. latifascia* (Walker). In the temperate regions of South America *S. frugiperda* and *S. cosmiodes* (Walker) are pests.

About half of the 30 *Spodoptera* species have been considered pests. No phylogeny of the genus has ever been constructed using modern cladistic techniques. To better understand the relationships between pest and non-pest species of *Spodoptera* and possible host plant relationships, a phylogenetic analysis of the genus is presented.

No comprehensive revision of *Spodoptera* on a world level is available. Brown & Dewhurst (1975) treated the African species of *Spodoptera*, giving keys to adults, larvae, and some pupae. They reviewed the taxonomic literature concerning generic synonyms of *Spodoptera* and the separation of *S. littoralis* from *S. litura* (Fabricius), discussed character states used to separate both species of adults and larvae, and gave a list of common names used in Africa for the economically important species. Larval host plants were discussed as well as species distributions. Todd & Poole (1980) treated the Western Hemisphere species of *Spodoptera* by providing a key to the adults, and illustrating the adult and male and female genitalia. These works cover 22 of the 30 species, but the other 8 species, including economically important species such as *S. litura* and *S. depravata* (Butler), have not been included in any faunal or revisionary work on *Spodoptera*. *Spodoptera descoinsi* Lalanne-Cassou & Silvain (Lalanne-Cassou & Silvain *in* Lalanne-Cassou, *et al.* 1994) was described from French Guiana and is closely related to *S. latifascia* and *S. cosmiodes*. *Spodoptera cosmiodes* was recently found to be a valid species and not a synonym of *S. latifascia* (Silvain & Lalanne-Cassou 1997). All three species are distinct in genitalic structures and pheromone composition.

The phylogeny presented in this paper was constructed using the parsimony program Hennig86, Version 1.5 (Farris 1988). A total of 24 characters were used including 6 binary and 18 multistate. Transformation series analysis (TSA) was used to construct character state trees of the multistate characters (Mickevich 1982). Character state trees were used to analyze 14 of the multistate characters. Four of the multistate characters were run ordered. Eight monophyletic clades containing 2 to 5 species were recognized. *Spodoptera exigua* was the most plesiomorphic and *S. frugiperda* was the sister species to the *dolichos, littoralis, evanida,* and *praefica* clades. Two outgroups were used based on results of a molecular systematics study of the Noctuidae (Mitchell 1998). A single tree was produced with a length of 143, a consistency index of 0.77, and a retention index of 0.91 (Fig. 3).

Databases were produced for the larval host plants, parasitoids, and predators of *Spodoptera*, as well as a bibliographic database in support of these. A specimen database was created for examined material. A gazetteer is provided for all localities recorded in this revision, including latitude and longtiude data when available. These are available on the internet at the Systematic Entomology Laboratory and the Department of Entomology, Smithsonian Institution websites.

Todd & Poole (1980) transferred *Spodoptera hipparis* (Druce) out of *Leucochlaena*. This genus is restricted to the Old World and its species superficially resemble *S. hipparis*, but the male and female genitalia of *S. hipparis* indicate that it is not congeneric with species of *Leucochlaena*. *Spodoptera hipparis* should not be included in *Spodoptera* because it shares no synapomorphies with *Spodoptera*, such as the large hair tuft on the female 8th segment. A review of New and Old World genera should be conducted to determine where *S. hipparis* should be placed. If no satisfactory generic placement can be found, a new one will be described to accommodate this species.

Literature Review

Spodoptera was described by Guenée (1852a) and included the following 7 species: *S. mauritia* (Boisduval), *S. abyssinia* (Guenée) (in *Ariathisa* (Poole 1989)), *S. acronyctoides* (a synonym of *S. mauritia*), *S. nubes* Guenée (a synonym of *S. mauritia*), *S. pecten* Guenée, *S. filum* Guenée (a synonym of *S. mauritia*), and *S. cilium* Guenée. He also created the unnecessary objective replacement name, *S. acronyctiformis* Guenée (1852b), for *S. acronyctoides* Guenée (Poole 1989). Three other species were originally described in *Spodoptera*, *S. evanida* Schaus (1914), *S. malagasy* Viette (1967) and *S. descoinsi* Lalanne-Cassou & Silvain (1994).

Two synonyms of *Spodoptera*, *Laphygma* and *Prodenia* were described by Guenée (1852a). *Laphygma* was synonymized by Turner (1920) and *Prodenia* was synonymized by Viette (1963). Guenée described the species *cycloides* (a synonym of *cilium*) and *macra* (a synonym of *frugiperda*), and placed the species *exigua, pygmae* (a synonym of *exigua*), and *frugiperda* in *Laphygma*. He described the species *tasmanica* (a synonym of *litura*), *ornithogalli, ciligera* (a synonym of *litura*), *eudiopta* (a synonym of *ornithogalli*), and *testaceoides* (a synonym of *littoralis*), and placed the species *androgea, commelinae* (a synonym of *dolichos*), and *retina* (a synonym of *littoralis*) in *Prodenia*.

Guenée (1852a) also described the genus *Xylomyges* in which he described the species *sunia*.

Hampson (1909) described *ochrea* and placed *eridania, sunia,* and *peruviana* in *Xylomyges.* Poole (1989) points out that *Spodoptera albula* (Walker) is the species that had been previously known as "*Spodoptera sunia* (Guenée)" however, the real *Xylomyges sunia* Guenée is actually a synonym of *Neogalea esula* Druce. All references relating to *Spodoptera sunia* prior to 1989 should be referred to *Spodoptera albula.*

I am not going to detail the works of Walker (1856, 1857a, 1857b, 1858, 1862a, 1862b, 1865a, 1865b, 1869, 1870) who described species of *Spodoptera,* but will summarize his results. Walker created 48 names of which 8 are valid (17%). He placed these species in 10 genera and used *Spodoptera* only once, in describing *S. insula* (a synonym of *cilium*).

Druce (*in* Godman & Salvin 1889) listed 4 species under both *Laphygma* and *Prodenia* for the Mexican and Central American fauna. No new species were described.

Hampson (1894) placed *littoralis* (*litura*) and *Catamecia minima* (Swinhoe) in *Prodenia,* and included *Spodoptera mauritia* and *Calogramma festiva* (Donovan). *Spodoptera picta* (Guérin-Méneville) is the subjective replacement name of *Calogramma festiva,* a junior primary homonym of *Phalaena festiva* Cramer (1775) (Sugi 1982). He also described two synonyms of *Spodoptera apertura* (Walker), *Prodenia synstictis* (Hampson 1896) and *Prodenia leucophlebia* (Hampson 1902). Hampson (1909) dealt with all of the *Spodoptera* species available to him at the time. He described *rubrifusa* (a synonym of *androgea*), and placed *dolichos, pulchella, androgea, litura, latifascia, ornithogalli, praefica,* and *marima* in *Prodenia.* He placed *umbraculata, pecten, Ariathisa abyssinia, compta, mauritia,* and *Diarsia postfusca* in *Spodoptera.* He placed *leucophlebia* (a synonym of *apertura*), *apertura, exempta, frugiperda, flavimaculata* (a synonym of *exigua*), and *exigua* in *Laphygma.* In the genus *Xylomyges,* he included *eridania, peruviana* (synonym of *ochrea*), *ochrea,* and *sunia* (*albula*). He also included *C. festiva.*

Turner (1920) gave descriptions of the *Spodoptera* species in Australia. He listed *Calogramma festiva* (*S. picta*), *Prodenia litura,* and the following *Spodoptera* species: *umbraculata, mauritia, leucophlebia* (=*apertura*), *exempta,* and *exigua.* Edwards (1996) lists the following species of *Spodoptera* from Australia: *picta, litura, mauritia, apertura, exempta, exigua,* and *umbraculata.*

Viette (1967) described and illustrated 6 species of *Spodoptera* from Madagascar. He described a new subspecies, *S. leucophlebia malagasy.* This is now recognized as a valid species, *S. malagasy* Viette (Poole 1989).

Brown & Dewhurst (1975) revised the *Spodoptera* species of Africa and the Near East. This is the most comprehensive treatment of *Spodoptera* for any region. They included descriptions of 8 species for both adults and larvae, treated 5 species of pupae and gave keys to these life stages. They discussed common names, distribution, characters to aid in identification, and host plants. They included illustrations of adults, larvae, pupae, spermatophores, male and female genitalia as well as other characters used in the keys.

Todd & Poole (1980) treated the *Spodoptera* species of the Western Hemisphere. They presented keys based on maculation and male genitalia. Fourteen species were treated, including discussions of characters used to identify them and their distributions. Adults and both male and female genitalia were illustrated.

Holloway (1989) discussed 8 species of *Spodoptera* from Borneo. He gave diagnoses, discussed their distribution, habitat preference, and biology including some host plant records. All adults were illustrated, including male genitalia, but not all female genitalia were illustrated. He listed 3 species from Mt. Kinabalu, Sabah (Holloway 1976); and the widespread pest species *S. mauritia* and *S. litura* from New Caledonia (Holloway 1979) and Norfolk Island (Holloway 1977). These pests were also listed by Robinson (1975) from Fiji.

Lalanne-Cassou *et al.* (1994) described a new species of *Spodoptera* from French Guiana that is closely allied to *S. latifascia.* They include a revised couplet for the key in Todd & Poole (1980) and information on the differences between the female sex pheromone of these two species. They also resurrected from synonymy *S. cosmiodes* based on differences in the genital morphology, mitochondrial DNA, pheromones, and behavior (Silvain & Lalanne-Cassou 1997).

Larval Host Plants

The common name for *Spodoptera* is "armyworm", because of the behavior of many species that move en masse from one location to another when searching for preferred hosts. Highly mo-

bile, large larvae may have a tendency to be more polyphagous than smaller sedentary larvae (Reavey 1993). Being highly mobile gives larvae the potential of a broader range of host plants (Berdegue & Trumble 1996). All clades have at least one pest that is a serious threat to agriculture in the world, except the *umbraculata* clade.

Certain clades (Fig. 3) can be classified with respect to host plant specificity and polyphagy. The *cilium* clade feeds on 10 or fewer plant species, most, but not all of which are grasses (Poaceae) and could be considered oligophagous. In the *umbraculata* clade larval host plants are known from only 2 species. The larva of *Spodoptera pectinicornis* (Hampson) is monophagous on *Pistia stratiotes* (L.) (water lettuce, Araceae), and *Spodoptera apertura* (Walker) has been collected in the field on tobacco in Zimbabwe and larvae have been reared from it, but this seems to be an isolated occurrence (Brown & Dewhurst 1975). Clade 21 is of Neotropical distribution and can be considered polyphagous, with the exception of *S. ochrea* (Hampson). The *exempta* clade could be considered polyphagous and they feed almost exclusively on Poaceae. In this clade, *S. triturata* (Walker) has been recorded only on sugar cane and rice. The *littoralis* clade is highly polyphagous, with the exception of *S. picta*. The *evanida* clade is oligophagous with *S. cosmiodes* feeding on 6 plant species and *S. latifascia* feeding on 8 species. The *praefica* clade could be considered polyphagous with the exception of *S. pulchella* (Herrich-Schäffer) and *S. marima* (Schaus) (1 host species each). No biological information is known for *S. roseae*.

Studies on host plant preference in pest species of *Spodoptera* have been conducted to examine the preference between crop hosts. The results are influenced by plants that the experimenters choose in these studies. In India, *S. exigua* preferred pea (*Pisum sativum* L.) in one study (Rawat *et al.* 1969) and in another it preferred alfalfa (*Medicago sativa* L.) (Verma *et al.* 1976), but these studies are not comparable because neither of these two hosts were compared to each other. In Egypt, four studies were conducted on host preference in *S. littoralis*, and castor (*Ricinus communis* L.) was preferred in all of them (Elbadry *et al.* 1971, Abdel-Salam *et al.* 1971, Harakly & Bishara 1974, Aboul Nasr *et al.* 1975). More recent studies of host preference have focused between natural hosts and crop hosts. Pest species such as *S. exigua*, *S. frugiperda*, and *S. latifascia* can develop on many hosts, but optimal development may take place on non-crop plants (Berdegue & Trumble 1996, Portillo *et al.* 1996). This is important when designing intercropping scenarios for control of *Spodoptera* pests. Weedy fields had lower numbers of *S. frugiperda* attacking sorghum than in weed free fields or where sorghum was intercropped with maize (Castro *et al.* 1989).

METHODS AND MATERIALS

Descriptions

DELTA (Descriptive Language for Taxonomy) is a computer program that enables systematists to gather descriptive systematic data and present it in a consistent, comparable manner (Dallwitz 1980; Dallwitz, *et al.* 1993). The descriptions for both adults and larvae were generated using DELTA. The key to the larvae was produced by DELTA. Keys to the adults were not produced by DELTA, but it was used as an aid to construct these keys.

Sources of Material Examined

The following is a list of acronyms of institutional or private collections used during this study. Acronyms from institutional collections follow Heppner & Lamas (1982).

AMNH	American Museum of Natural History, New York, New York, USA
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia
BM	Private collection of Bryant Mather, Clinton, Mississippi, USA
BMNH	The Natural History Museum (formerly the British Museum (Natural History)), London, England
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA
CNC	The Canadian National Collection, Research Branch, Agriculture Canada, Ottawa, Canada
CSU	Colorado State University, Ft. Collins, Colorado, USA
INBIO	Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica
MNHP	Muséum National d'Histoire Naturelle, Paris, France
MSU	Mississippi State University, Mississippi State, Mississippi, USA

ULK University of Louisville, Louisville, Kentucky, USA

USNM Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

VOB Private collection of Vitor O. Becker, Planaltina, D.F., Brazil

During the course of this study, types were searched for in the collections of the BMNH, CNC, MNHP, and USNM. If the type repository is listed as "unknown" in the type material section of the species descriptions, then it can be assumed that it is not in any of the collections that were searched.

Mapping

The maps of collecting localities (Figs. 522–543) were produced using the software Versamap for Windows (http://www.versamap.com). Versamap requires latitude and longitude in decimal format to plot the points on the maps. Latitude and longitude were obtained for collecting localities (label data) for the United States and its territories from the United States Geological Survey's (USGS) Geographic Names Information System (http://mapping.usgs.gov/www/gnis); for the rest of the world the National Imagery and Mapping Agency's (NIMA) GEOnet Names Server was used (http://164.214.2.59/gns/html/index.html). From these sources a Gazetteer of Spodoptera Collecting Localities database was produced which is available on the internet at the Systematic Entomology Laboratory and Department of Entomology, Smithsonian Institution websites. Localities marked "unknown" in the gazetteer were either not in the USGS and NIMA databases, or there were multiple localities with the same name, so it was impossible to infer the correct locality from the inadequate label data.

Databases

In support of this research on the world species of *Spodoptera* several databases were developed. Databases include those of larval plant hosts, parasitoids, and predators including a bibliographic database that supports the records found in these databases. Not all specimens examined were individually databased, but each locality from which specimens were examined is included in the Specimen Database. Specimens from the BMNH and MNHP were not individually databased as their holdings were too great. Specimens examined from the other institutions were databased and each specimen was given a unique number (bar code label or individual number label), and all label data, species identification, and repository where specimen is housed were recorded. A Gazetteer of *Spodoptera* Collecting Localities database was produced that includes the latitude and longitude of all collecting localities of *Spodoptera* that were examined during this study. All of these databases can be found on the internet at the Systematic Entomology Laboratory and Department of Entomology, Smithsonian Institution websites.

Larval Host Plants

The host plant data was compiled from the literature and specimens in collections. The *Review of Applied Entomology, Series A, Agricultural,* volumes 1 to 82 (1913–1994) was used to obtain most of the host plant records. A host plant record consists of the host plant, the *Spodoptera* species feeding on the host, and the country. The state was used for records in the United States. I tried to use the first time the record was mentioned in the literature. Many older records are based on obscure Agriculture reports and those of country and/or state Entomologists. I tried to duplicate these records by more recent, easily retrievable literature. Since *Spodoptera* are easily reared in the laboratory on a variety of hosts and artificial diets, many of the more common pests have been used as experimental animals. These records were ignored as the larvae may never have a chance to encounter what they were being fed in the laboratory in nature. I tried to base the larval host plant list on natural occurring records. All names were checked against the U. S. Department of Agriculture, Agricultural Research Service GRIN taxonomic database (www.ars-grin.gov/npgs/taxgenform.html) which provides the structure and nomenclature for the accessions of the National Germplasm System. Names were also checked in *Index Kewensis.*

Natural Enemies

Natural enemies refer to both parasitoids and predators of *Spodoptera.* The primary function of natural enemies from an agricultural perspective is that of biological control of pest species. Thompson (1946 a, b, c) compiled a list of the parasitoids of insect pests. Thompson & Simmonds

(1964) compiled a list of insect predators. The records for these lists were compiled from the papers in the *Review of Applied Entomology, Series A, Agricultural,* volumes 1–25 (1913–1937). I continued compiling *Spodoptera* records from volumes 26–82 (1938–1994). A parasitoid or predator record consists of the natural enemy, the *Spodoptera* species preyed upon, and the country. The state was used for records in the United States. I tried to use the first time the record was mentioned in the literature to keep redundancy to a minimum. Some records will have more than one citation if the older record is from an obscure publication, such as yearly reports from country and/or state agricultural departments and entomologists. Since several species of *Spodoptera* are easily reared, they have been used in laboratory experiments. I did not include records of parasitoids or predators being fed *Spodoptera* larvae when conducting compatibility studies, mass rearings in conjunction with biological control releases, or experiments on host preference.

The information presented should be used with caution and original papers should be consulted because their factual value should be evaluated. As mentioned in Thompson & Simmonds (1964), some of these records are erroneous, however excluding such references is not justified, since this is a compilation of published records.

Parasitoids

The nomenclature of the parasitoids was checked against the most recent catalogs and corrected from the original papers. Catalogs used were Krombein *et al.* (1979) for Hymenoptera and Stone *et al.* (1965), Guimarães (1971), Delfinado & Hardy (1977), Crosskey (1980), and Evenhuis (1989) for Diptera. Nomenclature of *Spodoptera* was also corrected from the original papers. For example, *S. litura* from Africa should be referred to as *S. littoralis.* Many parasitoids have been released from their country of origin for use in biological control in other countries. A record includes the *Spodoptera* host species, the parasitoid, and the country and/or state in the United States where the parasitoid was collected. The records are for specimens that were reared from field collected eggs, larvae, or pupae of *Spodoptera* species.

Predators

The nomenclature of the predators and *Spodoptera* species was updated from modern catalogues and corrected from the original papers. Catalogues used were Lorenz (1998 a, b) for the Carabidae (Coleoptera) and Henry & Froeschner (1988) and Aukema & Rieger (1996 a, b) for the Heteroptera. A record includes the *Spodoptera* host species, the predator, and the country and/or state that the predator was collected. The records are for specimens that were observed feeding on either eggs, larvae, or pupae of *Spodoptera* and were field collected.

Specimen Preparation

Whole body dissections and wing preparations were done by removing the left pair of wings and mounting them with white glue to a rectangular piece of acid free label paper and pinning them with the labels from the specimen. The right pair of wings were soaked in a 10% solution of hydrochloric acid for a few minutes then transferred to bleach until the wing scales turned white. The scales were then carefully removed from both surfaces of the wings and then transferred to acid fuchsin stain in 95% ethyl alcohol for 24 hours. The wings were then removed from the stain and rinsed in 95% ethyl alcohol. They were then transferred to xylene for 1 hour and mounted in Canada Balsam on a microscope slide with an appropriately sized cover slip. The whole body was put in 10% potassium hydroxide (KOH) in a test tube and heated for 30–40 minutes using a dry bath. The temperature was set so the specimen did not boil. The specimen was then cleaned and rinsed in distilled water and placed in a vial of 40% ethyl alcohol for study. After study, the whole body was placed in a 1/2 dram shell vial containing glycerine and permanently stored with the left pair of wings.

To prepare the genitalia the abdomen was broken off and placed in 95% ethyl alcohol to wet it, then it was placed in a test tube of 10% KOH and heated for 30–40 minutes (depending on size) using a dry bath. By first wetting the abdomen in alcohol it does not have a tendency to float in the KOH. The abdomen was then transferred to distilled water and cleaned of internal matter and scales. The abdominal pelt with genitalia attached was then placed in a solution of chlorazol black and distilled water until stained, (usually a few minutes depending on strength of stain), rinsed in distilled water, and then the genitalia were dissected from the abdomen. The abdominal pelt was slit up the right side with ventral side up and

any additional cleaning was done. The genitalia and abdomen were then stained in mercurochrome and rinsed in distilled water. The aedoeagus was dissected from the male genitalia and the vesica was everted with distilled water using a number 30 needle on a hypodermic syringe. The aedoeagus was then placed back in the chlorazol black until the vesica was lightly stained. After staining, the vesica was rinsed by shooting a stream of 99% isopropyl alcohol through it and then it was stored in isopropyl alcohol until slide mounting. The isopropyl alcohol hardens the vesica to help hold its shape. The abdomen and genitalia were then soaked in increasing strengths of 40%, 70%, and 95% ethyl alcohol for at least 2 hours each. They were then soaked in xylene for 1 hour and mounted in Canada Balsam. The abdomen was mounted under a separate cover slip from that of the genitalia. In some preparations the right valve of the male genitalia was removed and mounted under a separate cover slip. The same technique applies to the female. The coverslip over the male and female genitalia was supported by small thicknesses of plastic to prevent distorting the genitalia.

Photographs of genitalia were taken with a Leaf MicroLumina digital camera mounted on a Wild Photomakroskop M 400 stereo dissecting microscope. The images were enhanced with Adobe PhotoShop® 5.0 and imported into Adobe Illustrator® 6.0 to make the plates. Adult photographs are from 35 mm slides that were made into digital images by a Polaroid SprintScan 35 slide scanner. These images were manipulated in Adobe PhotoShop® 5.0 and imported into Adobe Illustrator® 6.0 to make the plates.

Morphological Terms

General adult morphology, wing venation, and forewing pattern follows the nomenclature of Davis (1989), Miller (1991), and Lafontaine (1998). Genitalic nomenclature is compiled from several sources based on my ideas of homology of genitalic parts within *Spodoptera*, especially the nomenclature concerning the male valve. Terminology of the male tegumen and its attached parts (excluding the valve) and the female genitalia follow Klots (1970) and Lafontaine (1998). The valve presented problems of homology between species of *Spodoptera.* The structures of the valve follow the terminology of Forbes (1954) and are shown in Figs. 304–305. There is still confusion in the literature concerning the structures of the valve. Table 1 lists different names used for homologous structures of the valve from various authors. The costa is the sclerotized dorsoproximal margin of the valve. The cucullus is the dorsoapical region of the valve and is distinct ventrally from the valvula except in *S. exigua.* The valvula is the ventrodistal portion of the valve and the apex is distinct, except in *S. exigua.* The anellifer is the membranous region in the central portion of the valve (Sibitani *et al.* 1954). In the central part of the inner surface of the valve there is a basal sclerite to which a muscle is attached to its dorsoproximal apex. This muscle controls the movement of the valve during copulation. In *Spodoptera* the basal sclerite is a plate with an oblique bar that can be variously modified (see character 12). From the basal sclerite arise two structures, the clasper proper and the ampulla. These 3 structures (basal sclerite, clasper proper, and ampulla) form the clasper. The clasper proper is the ventral projecting structure that lacks setae (Fig. 304). The clasper proper is present in clade 21 and is absent or reduced to a small dorsally projecting flap in the rest of *Spodoptera*. The ampulla is always setose and is the prominent elongate pointed process in the central sub-apical portion of the valve (Figs. 304–305). An exception is in *S. exempta,* where the clasper proper is the large elongate pointed process, and the ampulla is a minute setose bump at the base of the clasper proper (Fig. 62). The editum is a prominent area of rather large setae just dorsal to the apex of the sacculus and sitting in the anellifer. It can be a small patch (Fig. 362) or be quite conspicuous (Fig. 360). Near the basal portion of the costa is a variously modified setose structure that ranges from a small tubercle (Figs. 41, 45) to an elongate process (Figs. 39, 43–44), which I refer to simply as the costal process. This structure seems to be unique to *Spodoptera.* Bayer (1960) referred to this structure as the labis. The sacculus is the ventroproximal region of the valve and is usually more sclerotized than the valvula. Larval terminology follows that of Stehr (1987) and setal nomenclature follows Hinton (1946).

Describing the color of various body parts and wing patterns in Lepidoptera is difficult because these colors are usually a mosaic of individual scales of many different colors. When describing color I will use the dominant color of the individual scales making up that body part or wing pat-

Table 1. Comparison of terms used in the male valve. The homologous structure are terms used in the *Spodoptera* valve and follow Forbes (1954). The costal process is first used here (see text).

Reference	Structure	Homologous Structure	Reference	Structure	Homologous Structure
Sibitani, et al. (1954)	costa	costa	Lafontaine (1987)	-	costa
	-	editum		-	editum
	sacculus	sacculus		sacculus	sacculus
	valvula	valvula		-	valvula
	cucullus	cucullus		cucullus	cucullus
	harpe	basal sclerite		-	basal sclerite
	ampulla	ampulla		harpe	ampulla
	harpe	clasper		-	clasper
	-	costal process		-	costal process
Klots (1970)	costa	costa	Lafontaine and	-	costa
	editum	editum	Poole (1991)	-	editum
	sacculus	sacculus		sacculus	sacculus
	valvula	valvula		-	valvula
	cucullus	cucullus		-	cucullus
	-	basal sclerite		-	basal sclerite
	ampulla	ampulla		clasper	ampulla
	clasper	clasper		-	clasper
	-	costal process		-	costal process
Todd and Poole (1980)	costa	costa	Lafontaine (1998)	-	costa
	-	editum		-	editum
	-	sacculus		sacculus	sacculus
	valvula	valvula		-	valvula
	cucullus	cucullus		-	cucullus
	-	basal sclerite		-	basal sclerite
	clasper	ampulla		clasper	ampulla
	-	clasper		-	clasper
	ampulla	costal process			costal process

tern. If two or more colors are of approximately equal distribution the description will include each color. Individual moths within a species also show subtle variations in amount and intensity of colors. By describing only the dominant color, lengthy and confusing color descriptions can be avoided. Major variation in wing color and/or pattern will be discussed after each species description.

CLADISTIC ANALYSIS

The taxa analyzed included 30 species of *Spodoptera* and two outgroup taxa, *Galgula partita* Guenée and *Elaphria grata* Hübner. The outgroups were selected based on a noctuid phylogeny derived from molecular data (Mitchell 1998). Male genitalia of *G. partita* are illustrated in Figs. 307 and 368 and the genitalia of *E. grata* are illustrated in Figs. 306 and 369. Female genitalia of *G. partita* are illustrated in Figs. 401 and 433 and the genitalia of *E. grata* are illustrated in Figs. 400 and 432. These outgroups were used to test the monophyly of *Spodoptera*.

A total of 24 characters was used of which 6 were binary and 18 multistate. Character state distributions of the multistate characters were as follows: three characters with 3 states, three with 4, two with 5 states, two with 6 states, three with 9 states, three with 10 states and two with 11 states. Fifteen multistate characters were coded as character state trees (Characters 3–4, 7–13, 17–20, 22–23) (Figs. 4–17) (Mickevich 1982, Mickevich &

Weller 1990, Pogue & Mickevich 1990). Ordered multistate characters included 1 and 5–6. Data were analyzed using the Hennig86 parsimony program written by Farris (1988, Version 1.5).

Missing data affects the placement of the taxa that contain missing data on the tree, resulting in multiple trees. Four vesica characters (19–22) were not available for two taxa, *S. compta* (Walker) and *S. pectinicornis*. The missing data were eliminated by inferring character states based on the states of their nearest neighbors.

Transformation series analysis (TSA) was used to construct character state trees of the multistate characters (Mickevich 1982). TSA requires that character states of a multistate character are assigned to each taxon on an initial cladogram. The initial cladogram of this analysis was created by treating all multistate characters as unordered. This will be referred to as the unordered tree(s). The trace character option in MacClade, Version 3 (Maddison & Maddison 1992) was useful in analyzing character state change on a cladogram. By tracing character state change on a cladogram, character state trees can be developed (see Mickevich & Weller 1990 and Pogue & Mickevich 1990 for methods of character state tree development). Most character state trees are complicated and have multiple branches (Figs. 6, 9–10, 15–17), and others are more simple (Figs. 4–5, 7, 11–13). Hennig86 requires linear variables, so the character state trees must be transformed into linear variables. The method of transcribing non-linear character state trees into linear variables is termed ordinal coding (Mickevich & Weller 1990). For example, character 3 has five states (Fig. 4) with two state paths, the longest path consisting of four states (1-0-2-4), the shortest with two states (0-3). Ordinal coding produces two linear characters for each character state, one linear character defining the character state position on each of the paths. For character 3 (Fig. 4), state 1 is coded as 00 as the linear variable, state 0 is 10, state 2 is 20, state 4 is 30, and state 3 is 11. Since character state trees are ordered by how character states evolve on the cladogram, no assumption should be made about state "0" being plesiomorphic. More complicated character state trees with more paths will be represented by more than two linear characters. The untransformed or raw data are in Appendix I and the transformed data are in Appendix II. The untransformed data were used in the unordered analysis and the transformed data were used to produce the *Spodoptera* phylogeny. Character state trees are illustrated in Figs. 4–17.

In some instances when analyzing the character state trees more than one equally parsimonious character state tree could be produced. I found that if you ran each of the character state trees individually with the rest of the data, one of the character state trees would usually produce a shorter tree. If there was more than one choice of character state tree, I would use the one that produced the shortest tree. If all character state trees produced the same length tree, I chose the character state tree with the fewest paths.

To find the shortest trees the "mhennig*" option was used which constructs several trees, each by a single pass through the data and adding the taxa in a different sequence each time, and finally applies branch-swapping to each of the trees. The command "bb*" was then used which applies branch-swapping to each initial tree created by "mhennig*", but retains all trees up to the limit of space allocated by the computer.

Cladistic Results

The raw or untransformed data (Appendix I) were analyzed by treating all of the characters as unordered. This produced ten equally parsimonious trees with a length of 136 steps, a consistency index (CI) of 0.79 and a retention index (RI) of 0.89. This step was necessary to produce a cladogram on which to trace the character states of multistate characters in order to develop character state trees using TSA. The ten trees were identical except in the clades on the cladograms designated A–E (Figs. 1–2). Positional subtrees (Pogue & Mickevich 1990) were used to show the changes among the ten trees in Figs. 1–2.

The unordered trees had two distinct tree topologies. Each one is represented in Figs. 1–2. The tree numbers are those produced by Hennig86, plus one, so Tree 0 in Henning86 will be Tree 1, Tree 1 is Tree 2, etc. in Table 2. Five areas (A–E) on the trees were changing, resulting in the 10 trees. In Fig. 1, four areas (B–E) were changing to produce the four trees represented in Table 2. Tree 1, with positional subtree cladograms, A1, B1, C1, D1, E1 is the tree shown in Fig. 1. To interpret Tree 6, positional subtree cladograms B2, C3, and E2 would be substituted for B1, C1, and E1; Tree 8 would have B2, C3, and D3 substituted on Fig. 1; Tree 10 would have B2 and C3 substituted

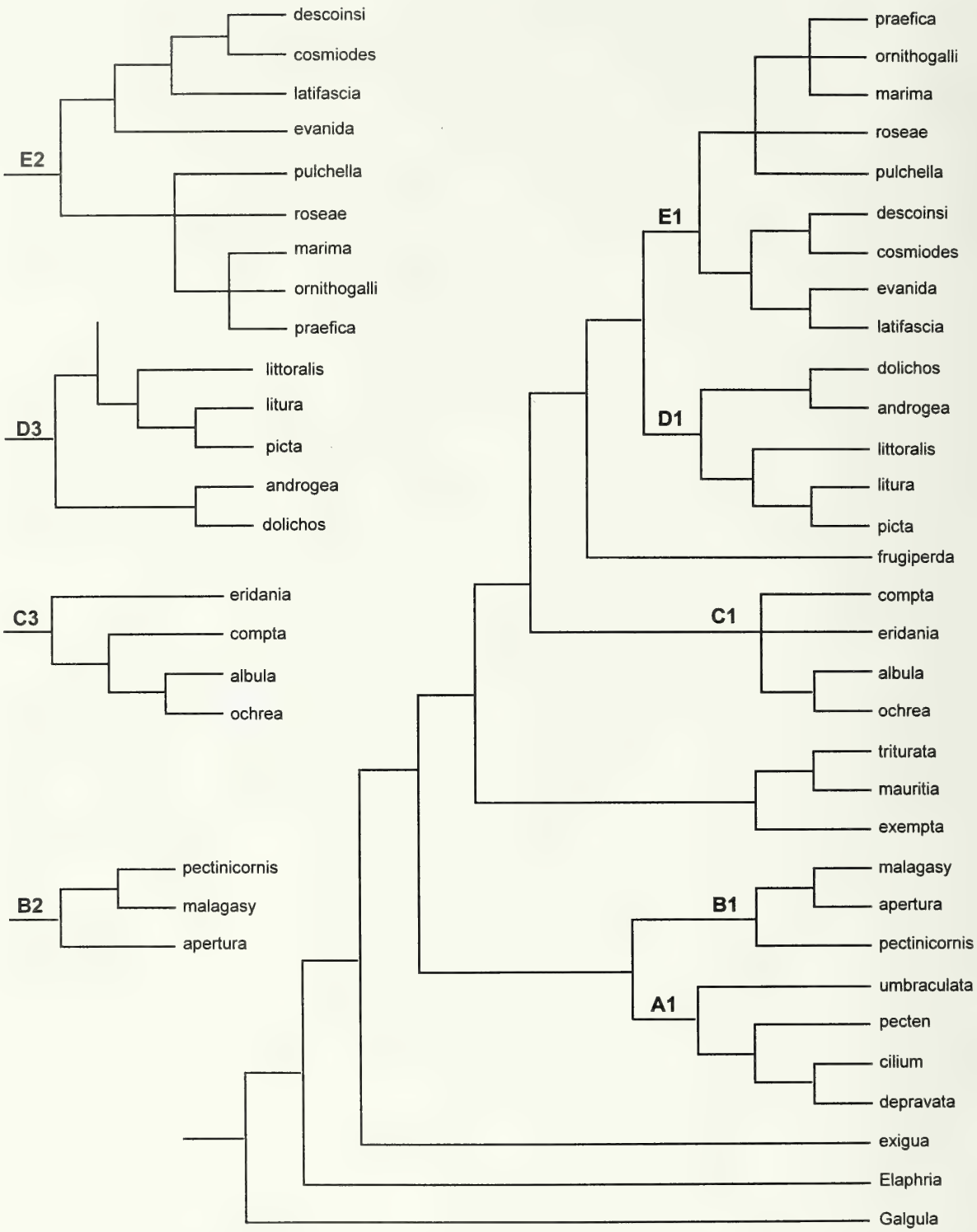


Fig. 1. Phylogeny of *Spodoptera* produced by Hennig86 using 30 species and 2 outgroups (*Elaphria* and *Galgula*) with *Elaphria* designated as the outgroup. Twenty-four characters were used all coded as unordered (Appendix I). Ten equally parsimonious trees were constructed (length = 136 steps, CI = 0.79, RI = 0.89). Positional subtrees were used to define 4 of the 10 trees (see text and Table 2).

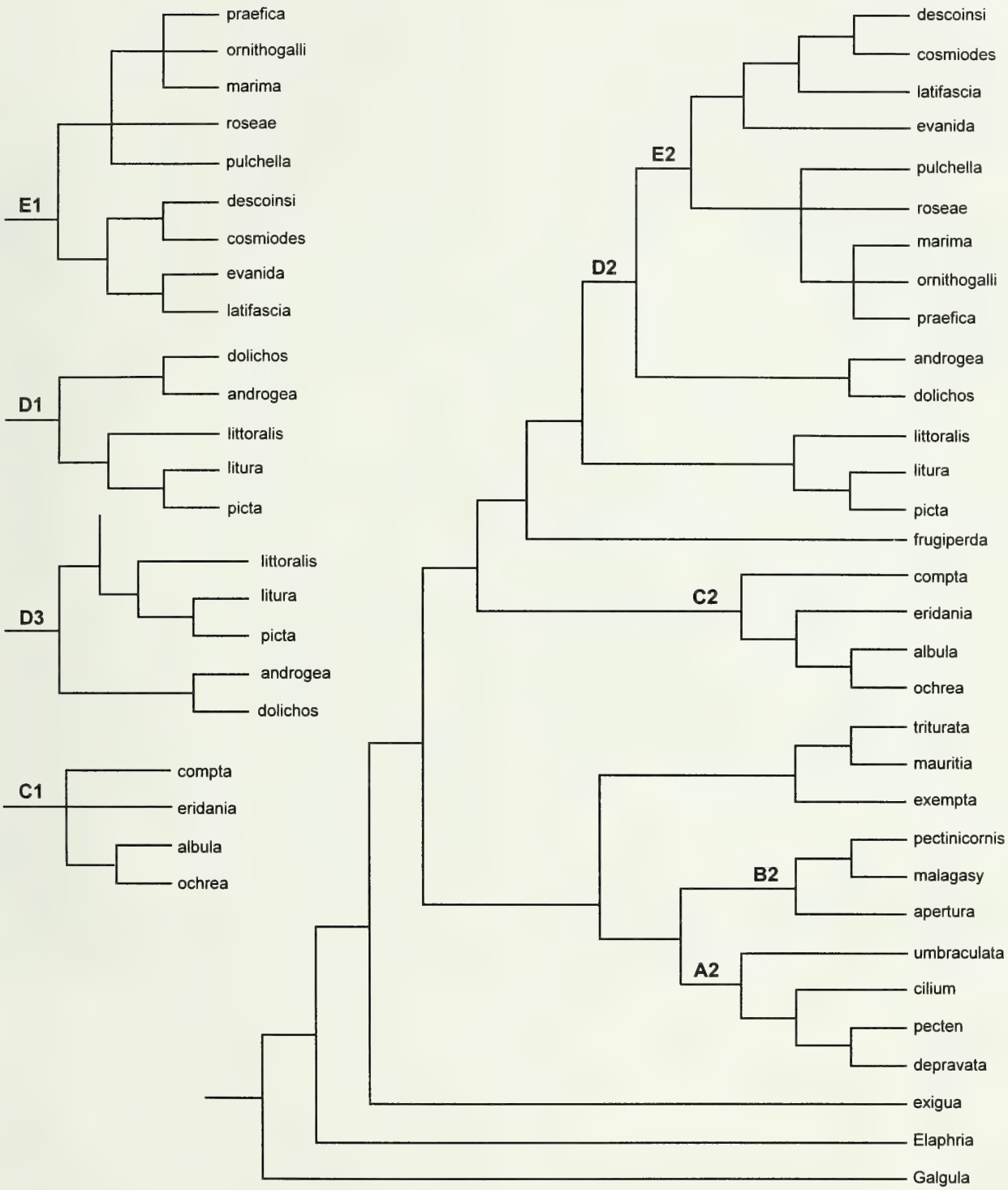


Fig. 2. Phylogeny of *Spodoptera* produced by Hennig86 using 30 species and 2 outgroups (*Elaphria* and *Galgula*) with *Elaphria* designated as the outgroup. Twenty-four characters were used all coded as unordered (Appendix I). Positional subtrees were used to define 6 of the 10 trees (see text and Table 2).

on Fig. 1. The tree topology with positional subtree cladogram A2 are Trees 2–5, 7, and 9 from the Hennig86 output; Tree 5 is shown in Fig. 2. Hennig86 trees 2–4, 7, and 9 can be interpreted as above by substituting the positional subtree cladograms in Table 2 on Fig. 2.

Using character state trees (Figs. 4–17), and transforming the character states to linear form using ordinal coding (Mickevich & Weller 1990), produced the data matrix in Appendix II. This data matrix was then analyzed, resulting in the final phylogeny shown in Fig. 3. Two trees were constructed with a length of 146 steps, a CI of 0.76, and a RI of 0.90. The *praefica* species group had two different topologies shown by the positional subtrees A1 and A2, which resulted in the two trees.

Monophyly of *Spodoptera* is supported by the synapomorphy of a dense cornutal patch on the vesica of the male aedoeagus and the female eighth segment covered with fine dense scales. The cladistic analysis of *Spodoptera* resulted in 8 monophyletic groups, with *S. exigua* the most plesiomorphic species. The *cilium, umbraculata,* and *exempta* species groups are Old World in origin and whose larval host plants are primarily grasses. The larvae have a chisellike cutting surface to the mandible as compared to a serrate or toothed cutting surface found in the remaining *Spodoptera* larvae. The exception is *S. pectinicornis* whose larvae have serrate mandibles. The *cilium* species group is defined by 4 characters (Appendix III, Clade 25). The *umbraculata* species group is defined by 2 male genitalic characters (Appendix III, Clade 27). The *exempta* species group is defined by a male genitalic character (Appendix III, Clade 18). Clade 21 is of Neotropical origin with *S. eridania* and *S. albula* extending into the Nearctic. This species group is defined by 6 characters (Appendix III, Clade 21) 5 from the male genitalia and 1 from the female genitalia. *Spodoptera frugiperda* is the sister species to the remaining species groups (*dolichos, littoralis, evanida,* and *praefica*). These groups have a similar forewing pattern (Figs. 253–303) with the M vein of the forewing being highlighted. All are New World in origin except the *littoralis* clade. The *dolichos* species group is defined by 3 male genitalic characters (Appendix III, Clade 17). The *littoralis* species group is defined by 5 male genitalic characters (Appendix III, Clade 15). The *evanida* species group is defined by 6 male genitalic characters (Appendix III, Clade 12). The *praefica* species group is defined by four male genitalic characters and one female genitalic character (Appendix III, Clade 9).

There are several species pairs of *Spodoptera* that were either considered the same or very closely related species. All of these pairs are sister species on the cladogram. These include *S. apertura* and *S. malagasy* which were originally described as subspecies, *S. littoralis* and *S. litura* were considered conspecific, as were *S. latifascia* and *S. cosmiodes*. The genitalia are virtually the same in *S. ornithogalli* and *S. marima*, but *S. marima* is not sexually dimorphic and is geographically isolated from *S. ornithogalli*. This is reflected in Fig. 3, subtree A1 as *S. marima* and *S. ornithogalli* form a trifurcation with Clade 11.

Table 2. Ten unordered trees produced by Hennig86 using mhennig* option. Tree structure analysis defined by positional subtree cladograms using Figs. 2–3 (see text).

Tree number	Positional subtree cladograms					Fig. number
1	A1	B1	C1	D1	E1	1
6	A1	B2	C3	D1	E2	1
8	A1	B2	C3	D3	E1	1
10	A1	B2	C3	D1	E1	1
2	A2	B2	C2	D1	E1	2
3	A2	B2	C2	D2	E1	2
4	A2	B1	C1	D3	E1	2
5	A2	B2	C2	D2	E2	2
7	A2	B2	C1	D1	E2	2
9	A2	B2	C1	D1	E1	2

Phylogenetic Characters

The following is a list of the characters used in reconstructing the phylogeny of *Spodoptera*. They are arranged in order of tagma. Binary characters have the plesiomorphic state coded as 0 and derived state as 1. Multistate characters are coded using ordinal coding (Mickevich & Weller 1990). Character state trees are illustrated for fourteen multistate characters (Figs 4–17). Two sets of character states are referred to. The states in **bold** are the raw data, presented in Appendix I.The states in *italics* are the transformed data coded ordinally

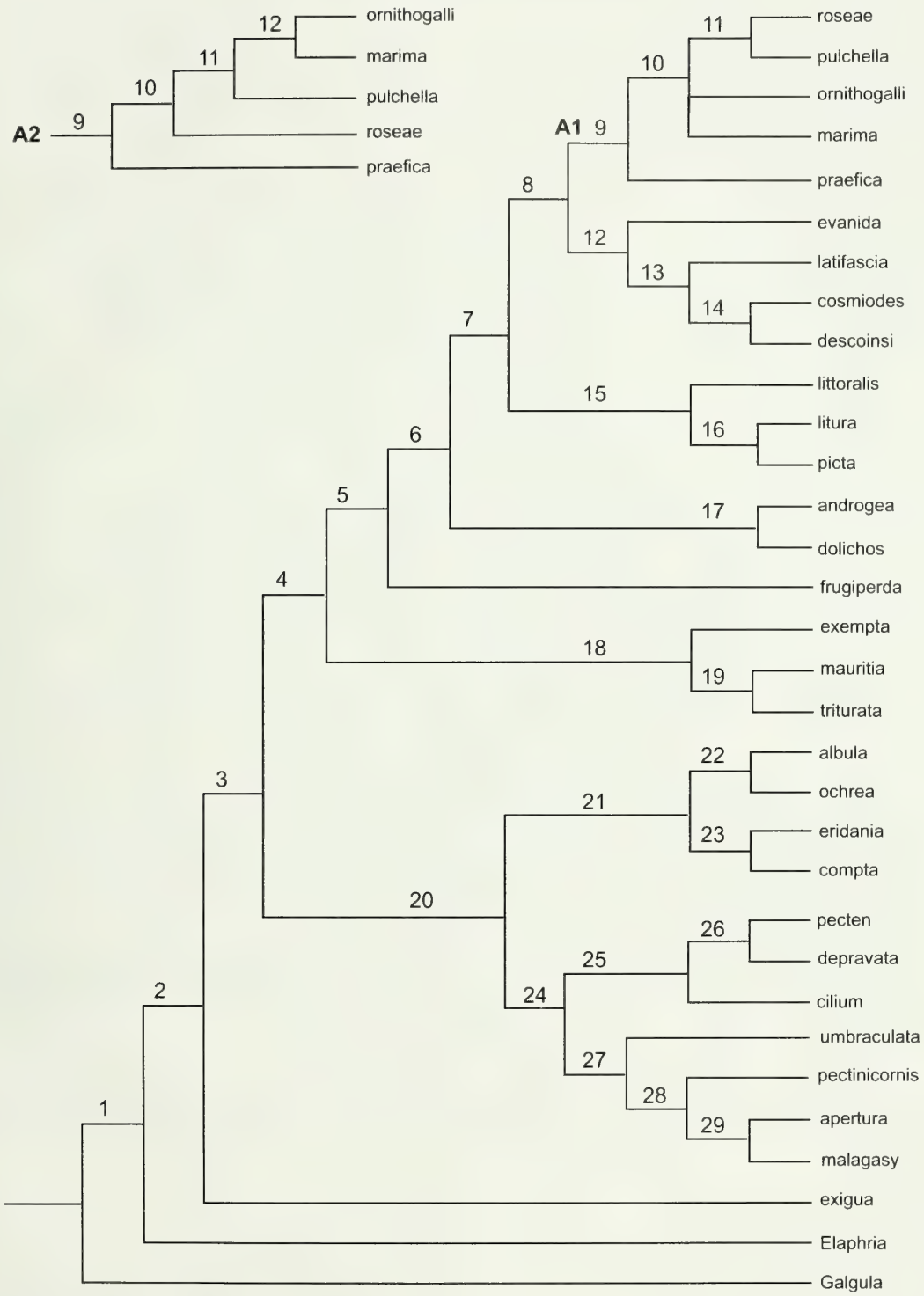
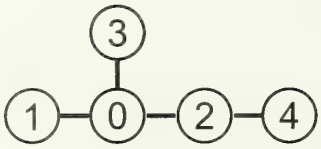


Fig. 3. Phylogeny of *Spodoptera* produced by Hennig86 using 30 species and 2 outgroups (*Galgula* and *Elaphria*) with *Galgula* designated as the outgroup. Twenty-four characters were used consisting of 6 binary and 18 multistate. Multistate characters were coded as 3 ordered and 15 defined by cladogram characters presented in Figs. 4–17 and in Appendix II. Two equally parsimonius trees were constructed (length = 143 steps, CI = 0.77, RI = 0.91) Positional subtrees A1 and A2 were used to define these trees.



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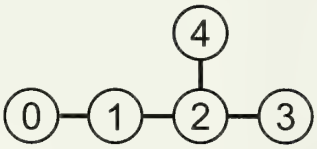

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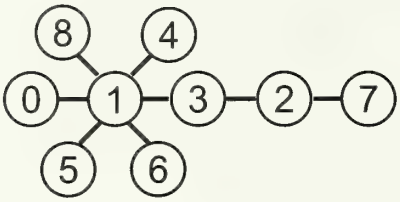

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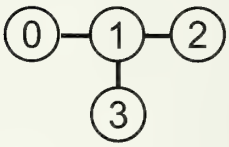

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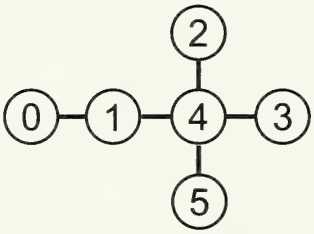

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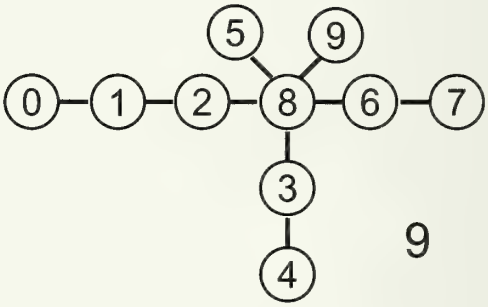

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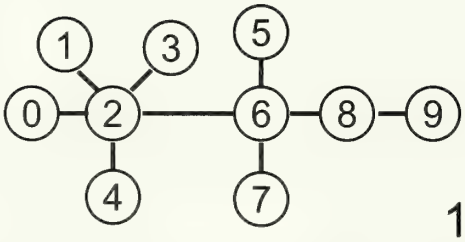

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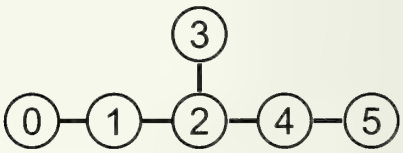

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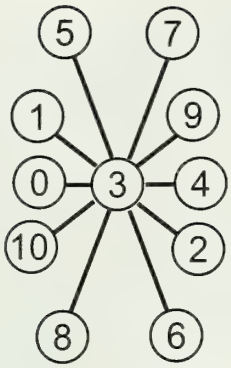
Figs. 4–11. Character state trees produced using TSA (see text) and used in data matrix in Appendix II. 4, Character 3. 5, Character 4. 6, Character 7. 7, Character 8. 8, Character 9. 9, Character 10. 10, Character 11. 11, Character 12.

to reflect the relationships in the character state trees and are presented in Appendix II.

Head

Antenna: *Character 1. Form of male flagellum.* **(0)** *(0):* filiform (Fig. 18); **(1)** *(1):* bipectinate (Fig. 19); **(2)** *(2):* serrate (Fig. 20). Most species of *Spodoptera* have a filiform antenna which is considered plesiomorphic. Bipectinate antennae arose twice, in Clade 24 and in *S. roseae* (Fig. 3). It is possible that the bipectination in Clade 24 is not homologous with that in *S. roseae*. Serrate antennae arose twice, in *S. cilium* and in Clade 29 (*S. apertura* and *S. malagasy*). The character was treated as ordered. *CI = 0.50*



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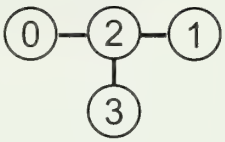

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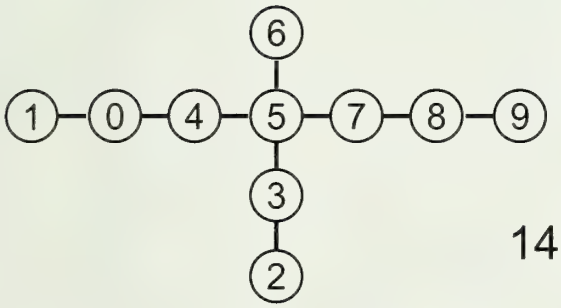

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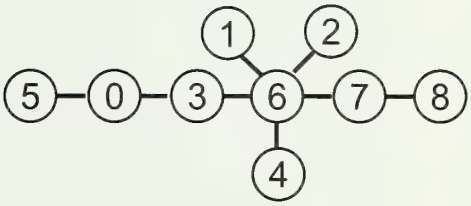

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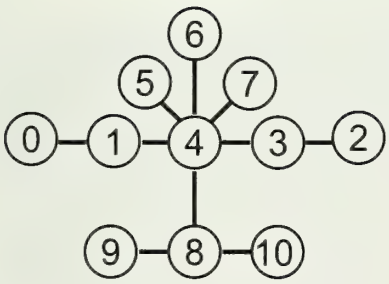

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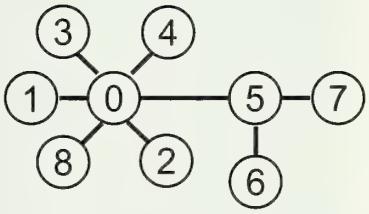

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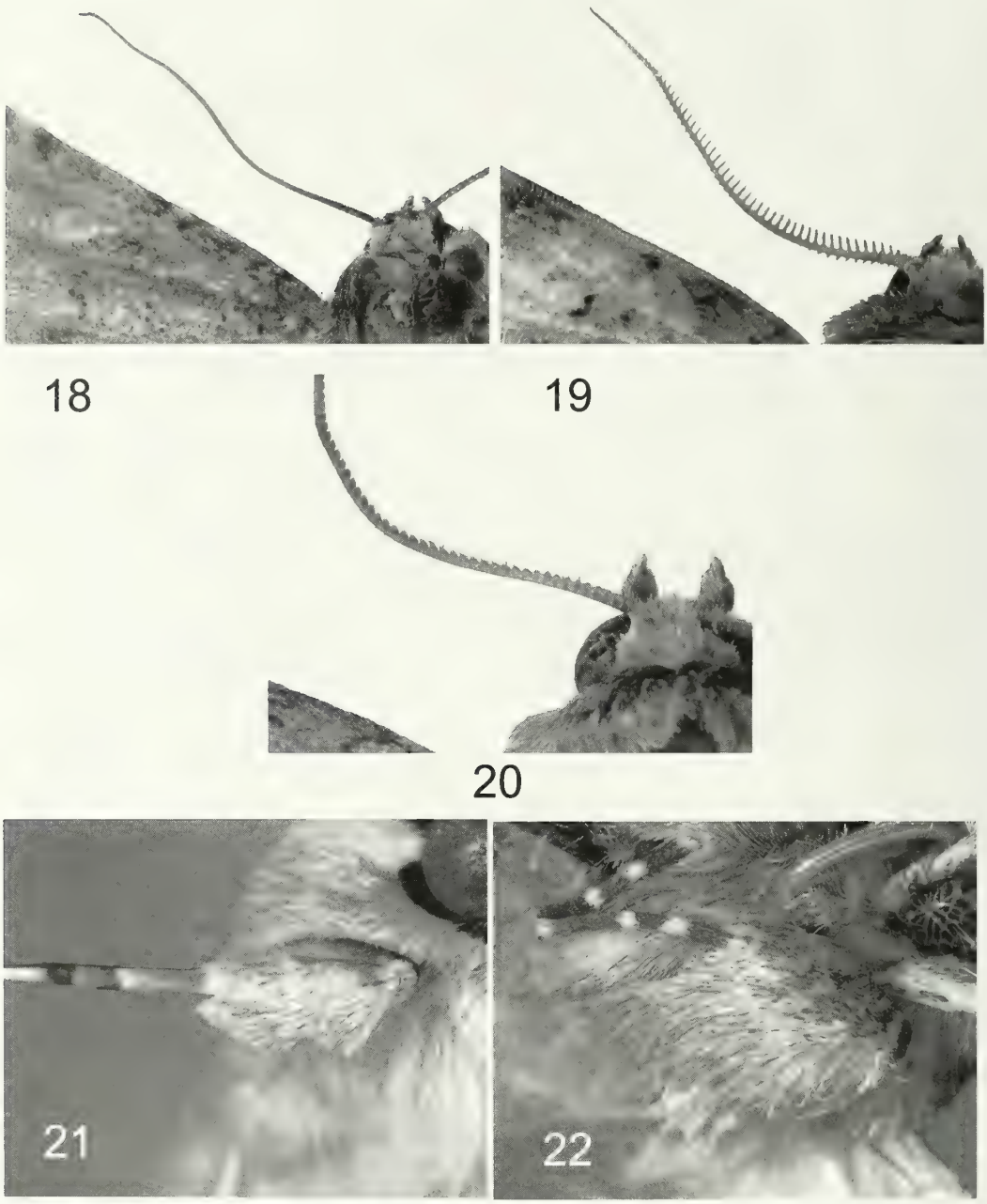
Figs. 12–17. Character state trees produced using TSA (see text) and used in data matrix in Appendix II. 12, Character 13. 13, Characters 17 and 22. 14, Character 18. 15, Character 19. 16, Character 20. 17, Character 23.

Thorax

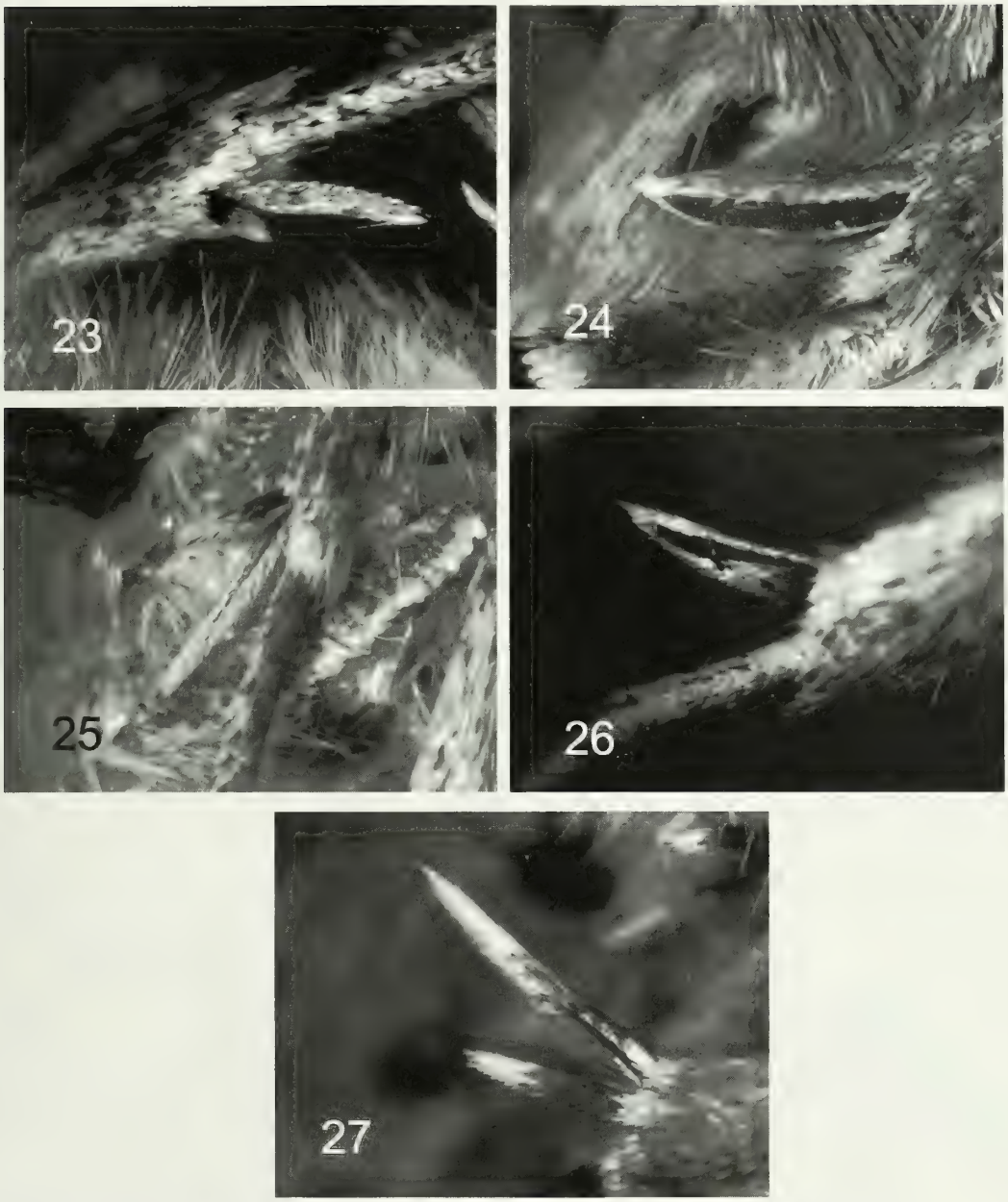
Prothoracic tibia: *Character 2. Length of lateral scale tufts.* **(0)** *(0):* not extending beyond first tarsal segment (Fig. 21); **(1)** *(1):* extending beyond first tarsal segment (Fig. 22). The scales of the prothoracic tibia are elongate and extend beyond the first tarsal segment in *S. mauritia* and *S. triturata*, which is a good character to separate them from the rest of *Spodoptera*. *CI = 1.00.*

Mesothoracic tibia: *Character 3. Tibial spur scaling.* **(0)** *(20):* spurs completely scaled (Fig. 23); **(1)** *(10):* mediolateral surface broadly devoid of scales on both spurs (Fig. 24); **(2)** *(30):* mediolateral surface thinly devoid of scales on both spurs (Fig. 25); **(3)** *(21):* mediolateral surface devoid of



Figs. 18–20. Antenna: Character 1, form of male flagellum. 18, Filiform, state 0, *S. exigua*. 19, Bipectinate, state 1, *S. pectum*. 20, Serrate, state 2, *S. cilium*. Figs. 21–22. Prothoracic tibia: Character 2, length of lateral scale tufts. 21, Not extending beyond first tarsal segment, state 0, *S. eridania*. 22, Extending beyond first tarsal segment, state 1, *S. mauritia*.

scales on large spur (Fig. 26); **(4)** *(00):* internal surface at base thinly devoid of scales on large spur (Fig. 27). The lack of scales on the male mesothoracic tibial spurs of some species was first mentioned by Zimmerman (1958). Spurs can be completely scaled or have varying degrees of bare areas on one or both spurs. Viette (1967) and Brown & Dewhurst (1975) used this character in keys to Madagascan and African *Spodoptera*. Character state tree - Fig. 4. *CI = 0.50.*



Figs. 23–27. Mesothoracic tibia: Character 3, tibial spur scaling. 23, Spurs completely scaled, state 0, *S. eridania.* 24, Medio-lateral surface broadly devoid of scales on both spurs, state 1, *S. mauritia.* 25, Medio-lateral surface thinly devoid of scales on both spurs, state 2, *S. exigua.* 26, Medio-lateral surface devoid of scales on large spur, state 3, *S. albula.* 27, Internal surface at base thinly devoid of scales on large spur, state 4, *S. roseae.*

Male Genitalia

Uncus: *Character 4. Width.* **(0)** *(10):* wide, constant throughout length (Fig. 28); **(1)** *(00):* narrow at base, wide medially to produced apex (Fig. 29); **(2)** *(20):* widest at base, gradually narrowing to apex (Fig. 30); **(3)** *(30):* narrowest at base, widest distally (Fig. 31). **(4)** *(21):* very wide, gradually narrowing to apex (Fig. 32). Most *Spodoptera* have an uncus that is widest at base and gradually narrowing to apex. Some Old World species have developed an uncus with a wide distal half, which

arose on Clades 19 and 25 (Fig. 3). *Spodoptera umbraculata* has a unique uncus shape that is very wide and gradually narrows to its apex (Fig. 32). Character state tree - Fig. 5. *CI = 0.80.*

Scaphium: *Character 5. Form and amount of sclerotization.* **(0)** *(0):* absent (Fig. 306); **(1)** *(1):* elongate, weakly developed (Fig. 33); **(2)** *(2)*: elongate, well sclerotized (Fig. 34). The tuba analis is the posterior part of the digestive tract and is supported by the dorsal scaphium (Klots 1970). In Clade 21 the scaphium is well sclerotized and elongate. This character was treated as ordered, with (0) as the plesiomorphic state. *CI = 1.00.*

Tegumen: *Character 6. Lateral projections of tegumen.* **(0)** *(0):* lacking a pair of projecting arms on upper third (Fig. 35); **(1)** *(1):* lateral swellings at basal two-thirds (Fig. 36); **(2)** *(2)*: with a pair of projecting arms on upper third (Fig. 37). In Clade 21 the lateral edge of the tegumen is modified from the state found in other *Spodoptera.* It is swollen in *S. compta* and *S. ochrea* and has prominent projecting arms in *S. eridania* and *S. albula.* This character was treated as ordered, with 0 as the plesiomorphic state. *CI = 0.67.*

Costal process: *Character 7. Shape.* **(0)***(011):* absent (Fig. 38); **(1)** *(111):* elongate, narrow (Fig. 39); **(2)** *(311):* short, straight, narrow (Fig. 40); **(3)** *(211):* a minute knob (Fig. 41); **(4)** *(110):* short, wide (Fig. 42); **(5)** *(112):* elongate, wide, slightly curved (Fig. 43); **(6)** *(121):* elongate, wide, well sclerotized (Fig. 44); **(7)** *(411):* a small swelling, no distinct process (Fig. 45); **(8)** *(101):* medium length and width (Fig. 46). The costal process is located subbasally on the costa of the valve. It is found in all species of *Spodoptera,* except *S. exigua,* where it may have been secondarily lost. It has many forms, from a minute knob (Fig. 41) or small swelling (Fig. 45) to an elongate, well sclerotized process (Fig. 44). In Todd & Poole (1980) this structure was misinterpreted as the ampulla. Character state tree - Fig. 6. *CI = 0.80.*

Character 8. Location on costa. **(0)** *(00):* absent (Fig. 47); **(1)** *(10):* at base of costa on inner edge (Fig. 48); **(2)** *(20)*: in middle of costa (Fig. 49); **(3)** *(11):* at base of costa along margin (Fig. 50). The costal process can be located on the margin, middle, or inner edge of the costa. Character state tree - Fig. 7. *CI = 1.00.*

Cucullus: *Character 9. Form.* **(0)** *(11):* distinct from valve (Fig. 51); **(1)** *(01):* pointed (Fig. 52); **(2)** *(20):*broadly rounded (Fig. 53); **(3)** *(31):* curved at costal apex, outer margin straight (Fig. 54); **(4)** *(21):* evenly rounded from costal apex to valvula apex (Fig. 55); **(5)** *(22):* truncate, forming almost a right angle at costal apex, outer margin straight (Fig. 56). The cucullus is the dorsodistal area of the valve. The outer margin varies from broadly rounded to truncate. Character state tree - Fig. 8. *CI = 0.63.*

Ampulla: *Character 10. Form.* **(0)** *(0000):* elongate, sinuate process, apex pointed (Fig. 57); **(1)** *(1000):* elongate process bent at a right angle at 2/3 length (Fig. 58); **(2)** *(2000):* elongate, narrow, slightly curved, apex round (Fig. 59); **(3)** *(3100):* short, thumb-shaped lobe, apex round (Fig. 60); **(4)** *(3200):* short, triangular shaped lobe, apex round (Fig. 61); **(5)** *(3010):* minute lobe (Fig. 62); **(6)** *(4000):* elongate, slightly curved with a pointed produced apex (Fig. 63); **(7)** *(5000):* elongate, slightly curved with an angulate pointed apex (Fig. 64); **(8)** *(3000):* elongate, slightly curved with a decurved apex (Fig. 65); **(9)** *(3001):* elongate, broad, curved with a decurved apex (Fig. 66). The ampulla is a structure that has been confused in the literature (Table 1). The ampulla is part of the clasper in the broad sense (Forbes 1954) and is dorsodistal from the basal sclerite (Figs. 67–76) to which a muscle is attached (Fig. 70, m). The ampulla is the transverse costal process with fine sensory setae and the sclerotized ventrodistal process is the clasper proper (Figs. 60–63, amp, cl). In most species of *Spodoptera* only the ampulla is present. In *S. exempta* the ampulla is a small knob located at the base of a well developed clasper (Fig. 62). Character state tree - Fig. 9. *CI = 1.00.*

Basal sclerite of clasper: *Character 11. Form.* **(0)***(0110):* short, crescent-shaped (Fig. 67); **(1)** *(1010):* oblique bar (Fig. 68); **(2)** *(1110):* a narrow plate with an oblique bar at proximal end (Fig. 69); **(3)** *(1111):* an elongate plate with costal and oblique bars joined to form a horizontal X (Fig. 70); **(4)** *(1210):* a broad plate with an oblique bar at proximal end (Fig. 71); **(5)** *(2100):* a quadrate plate with slightly sclerotized costal bar and an elongate horizontal bar (Fig. 72); **(6)** *(2110):* plate reduced, costal and oblique bars form an obtuse angle (Fig. 73); **(7)** *(2120):* an oblong plate, costal and oblique bars form an acute angle (Fig. 74); **(8)** *(3110):* a rectangular plate with costal and oblique bars joined to form a horizontal X (Fig. 75); **(9)** *(4110):* a reduced plate, costal bar curved and joining oblique bar to form an inverted Y (Fig. 76). The basal sclerite of the clasper, in the broad

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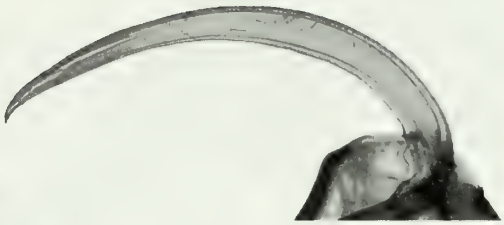

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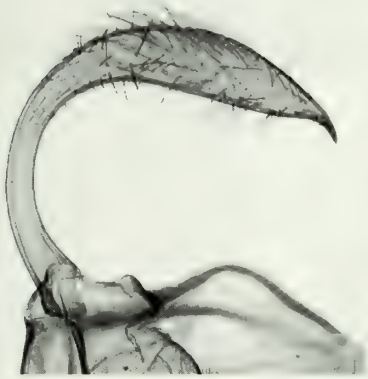

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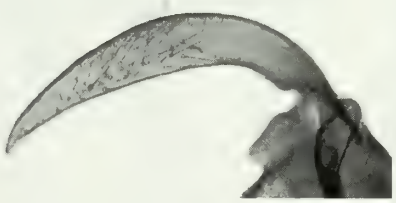

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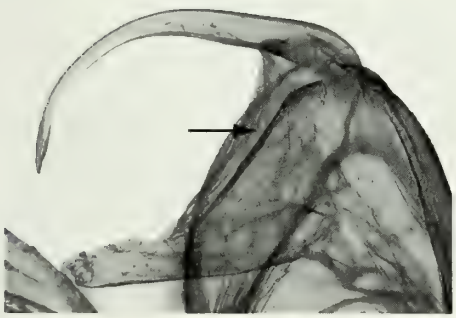

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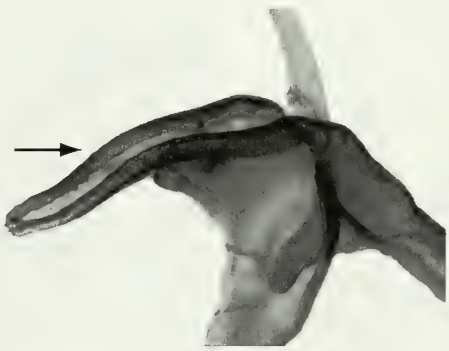

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Figs. 28–32. Uncus: Character 4, width. 28, Wide, constant throughout length, state 0, *Galgula partita* Guenée. 29, Narrow at base, wide medially to produced apex, state 1, *Elaphria grata* Hübner. 30, Widest at base, gradually narrowing to apex, state 2, *S. albula*. 31, Narrowest at base, widest distally, state 3, *S. mauritia*. 32, Very wide, gradually narrowing to pointed apex, state 4, *S. umbraculata*. Figs. 33–34. Scaphium: Character 5, form and amount of sclerotization. 33, Elongate, weakly developed, state 1, *S. evanida*. 34, Elongate, well sclerotized, state 2, *S. eridania*.

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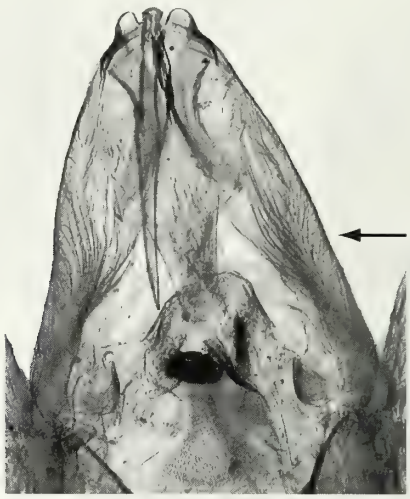

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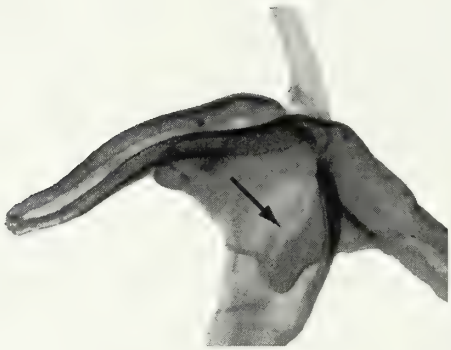

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Figs. 35–37. Tegumen: Character 6, lateral projections of tegumen. 35, Lacking a pair of projecting arms on upper third, state 0, *S. ornithogalli.* 36, Lateral swellings at basal two-thirds, state 1, *S. ochrea.* 37, Pair of projecting arms on upper third, state 2, *S. eridania.*

sense, is defined as the sclerite to which the valve muscle is attached. In *Spodoptera* the point of attachment is a small dorsocostal process (Fig. 70, m). Character state tree - Fig. 10. *CI = 0.90.*

Clavus: *Character 12. Shape.* **(0)** *(01):* a large, spiny, ellipitical lobe (Fig. 307); **(1)** *(11):* absent (Fig. 77); **(2)** *(21):* a minute round projection (Fig. 78); **(3)** *(20):* elongate, finger-shaped (Fig. 79); **(4)** *(31):* large, club-shaped, base narrower than apex (Fig. 80); **(5)** *(41):* short, round, covered with setae (Fig. 81). The clavus is a small separate organ between the base of the valve and juxta bearing sensory setae. It is absent in the more plesiomorphic *Spodoptera,* except in *S. pectinicornis, S. apertura,* and *S. malagasy,* and *S. mauritia* where it is a minute round projection. This character state is also shared with *S. frugiperda* and the *littoralis* species group. Character state tree - Fig. 11. *CI = 0.71.*

Sacculus: *Character 13. Shape.* **(0)***(01111):* cylindrical with heavily scelerotized triangular apex (Fig. 82); **(1)** *(10111):* quadrate (Fig. 83); **(2)** *(12111):*

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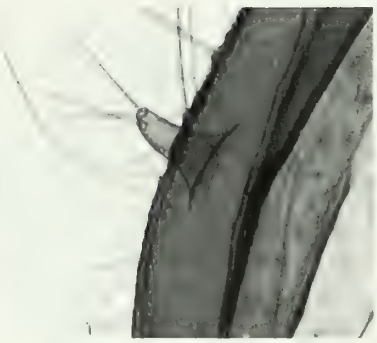

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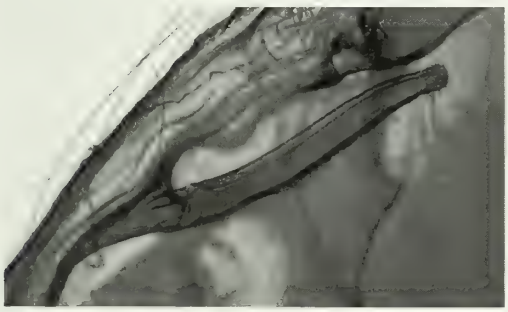

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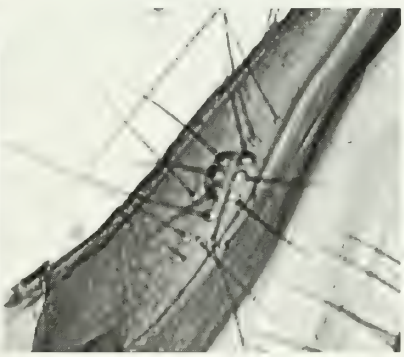

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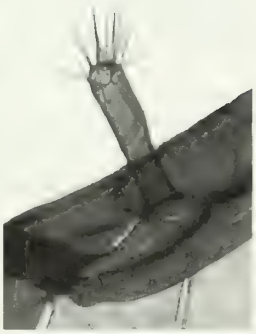

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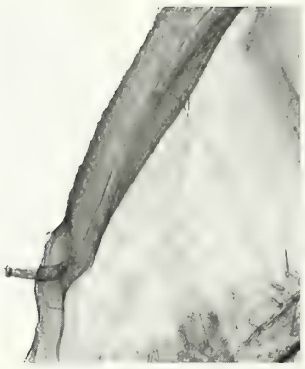
Figs. 38–46. Costal process: Character 7, shape. 38, Absent, state 0, *S. exigua.* 39, Elongate, narrow, state 1, *S. albula.* 40, Short, straight, narrow, state 2, *S. triturata.* 41, A minute knob, state 3, *S. cilium.* 42, Short, wide, state 4, *S. eridania.* 43, Elongate, wide, slightly curved,state 5, *S. picta.* 44, Elongate, wide, well sclerotized, state 6, *S. latifascia.* 45, A small swelling, no distinct process,state 7, *S. exempta.* 46, Medium length and width, state 8, *S. praefica.*



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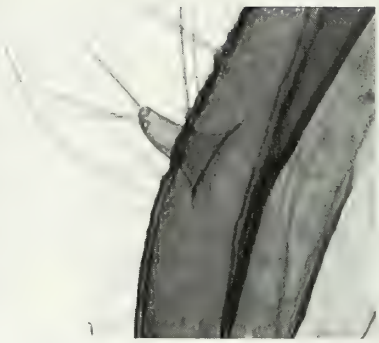

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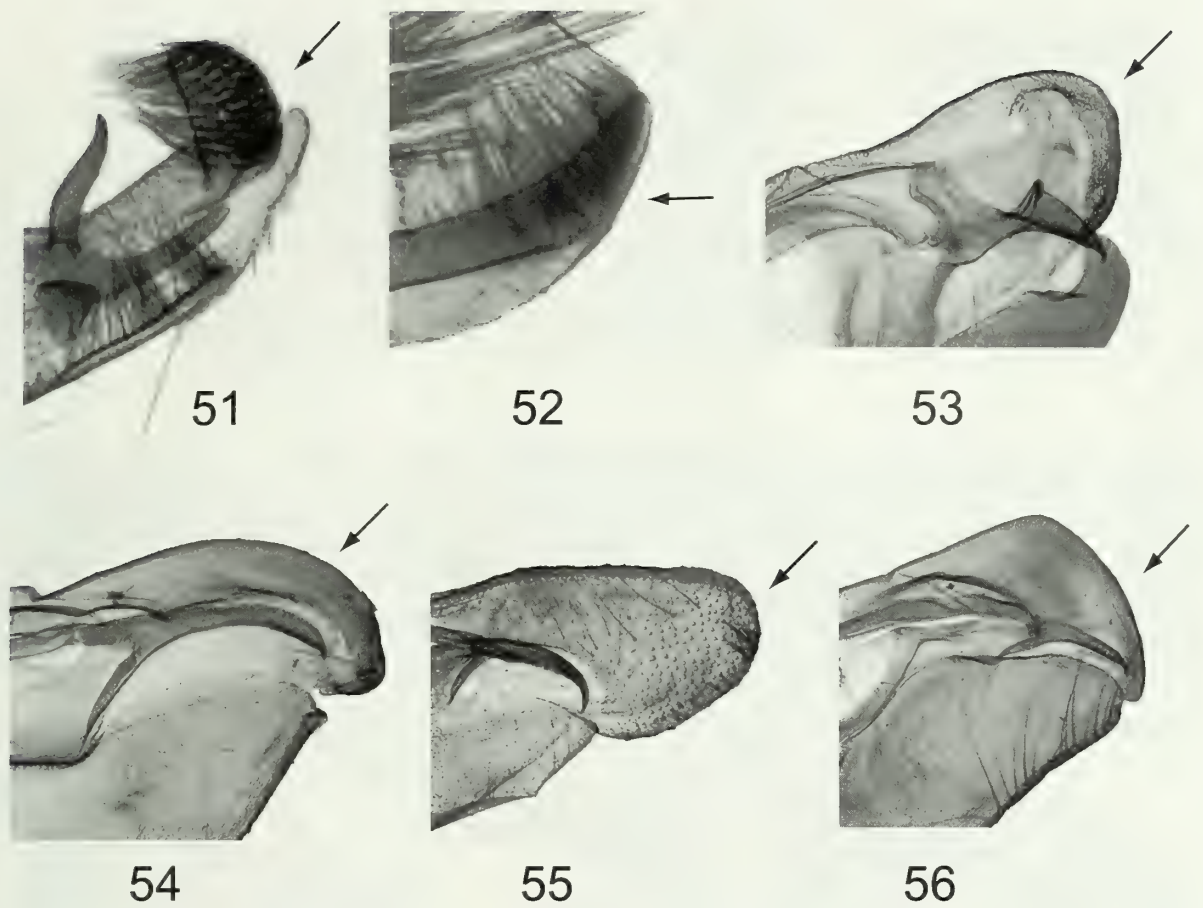
Figs. 47–50. Costal process: Character 8, location on costa. 47, Absent, state 0, *S. exigua.* 48, At base of costa on inner edge, state 1, *S. picta.* 49, In middle of costa, state 2, *S. triturata.* 50, At base of costa along margin, state 3, *S. mauritia.*

broad to half its length, tapering distally (Fig. 84). **(3)** *(11111):* rectangular, proximal margin wider than distal (Fig. 85); **(4)** *(21111):* trapezoidal, dorsal margin angulate (Fig. 86); **(5)** *(11011):* elongate, basal notch, widest at one-quarter length, gradually tapered to apex (Fig. 87); **(6)** *(11211):* elongate, basal notch, widest at one-third length, abruptly tapered to apex (Fig. 88); **(7)** *(11101):* triangulate (Fig. 89); **(8)** *(11121):* rectangular, slightly constricted at two-thirds length, apex indented (Fig. 90); **(9)** *(11110):* quadrate, apex tapered distally (Fig. 91); **(10)** *(11112):* rectangular, apex truncate dorsally, an elongate taper ventrally (Fig. 92). The sacculus is the ventrobasal portion of the valve which is more sclerotized ventrally and more membranous dorsodistally where it is clothed with setae. Various forms are present that define the different clades (Appendix III). Character state tree - Fig. 12. *CI = 1.00.*

Valvula: *Character 14. Ventral margin shape.* **(0)***(0):* smooth, setae not originating on short protuberances (Fig. 93); **(1)** *(1):* scalloped, setae originating on short protuberances (Fig. 94). The ventral margin of the valvula can be smooth or scalloped with setae arising on short protuberances. The scalloped edge is found in *S. frugiperda* and all of its sister taxa (Fig. 3). *CI = 1.00.*

Character 15. Width. **(0)***(0):* narrower than cucullus (Fig. 93); **(1)** *(1):* wider than cucullus (Fig. 94). The width of the valve also divides *Spodoptera* into *S. frugiperda* and all of its sister taxa. *CI = 0.33.*

Character 16. Valvular indentation. **(0)** *(0):* absent (Fig. 95); **(1)** *(1):* present (Fig. 96). Bayer (1960) recognized the valvular indentation just



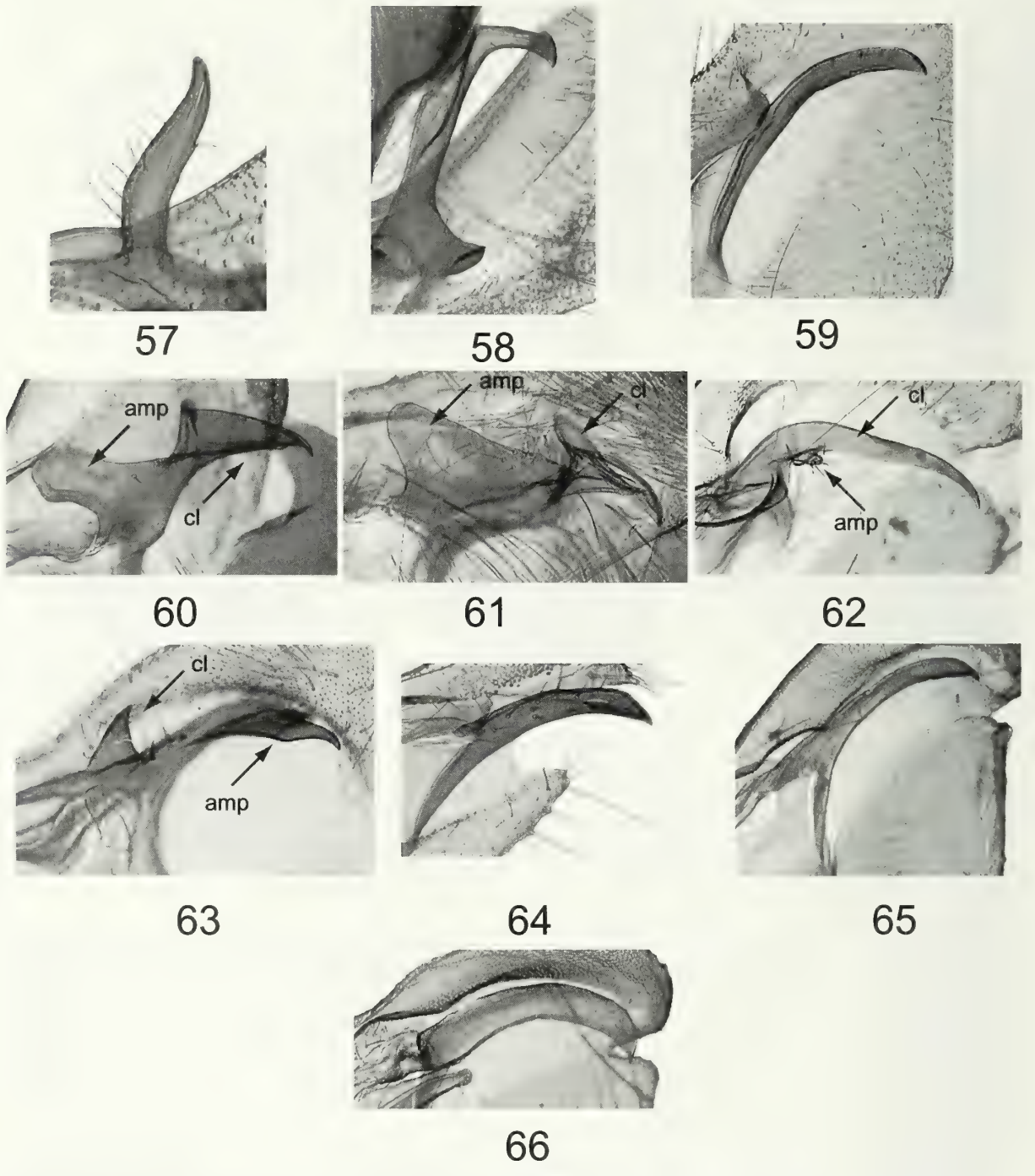
Figs. 51–56. Cucullus: Character 9, form. 51, Distinct from valve, state 0, *G. partita.* 52, Pointed, state 1, *E. grata.* 53, Broadly rounded, state 2, *S. albula.* 54, Curved at costal apex, outer margin straight, state 3, *S. androgea.* 55, Evenly rounded from costal apex to valvula apex, state 4, *S. mauritia.* 56, Truncate, forming almost a right angle at costal apex, outer margin straight, state 5, *S. frugiperda.*

below the juncture of the basal sclerite and sacculus. It is present in *S. frugiperda* and all of its sister taxa. *CI = 1.00.*

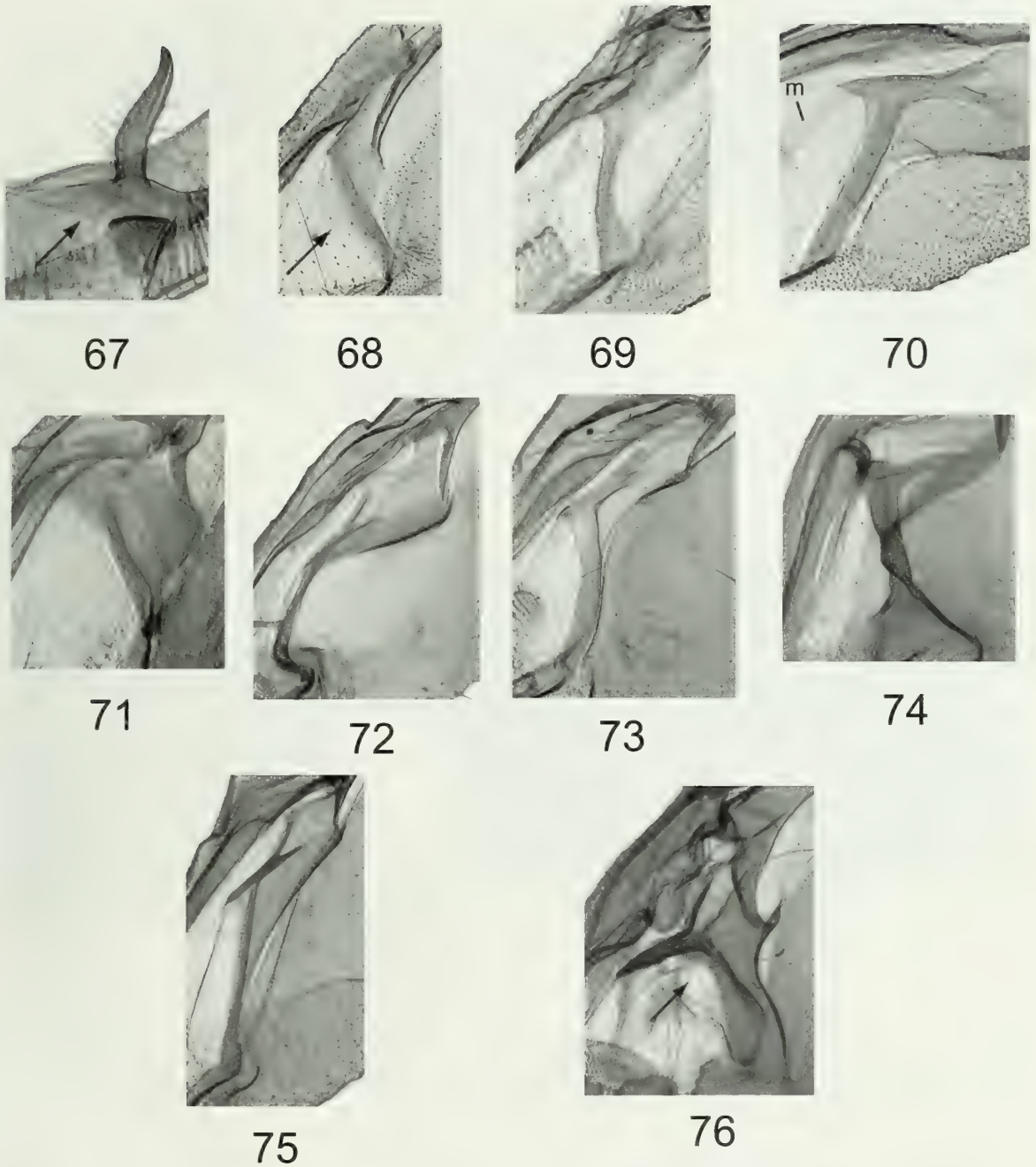
Coremata: *Character 17. Number of lobes.* **(0)***(00):* absent (Fig. 97); **(1)** *(20):* no distinct lobe, appressed against sacculus (Fig. 98); **(2)** *(10):* single lobe (Fig. 99); **(3)** *(11):* double lobe (Fig. 100). Coremata are large lobes covered with long fine hairs that are attached basally to the dorsal region of the valve. The coremata disperse pheromones during mating. All *Spodoptera* have coremata with varying degrees of development. In the *cilium* and *umbraculata* clades the coremata are reduced and closely appressed to the valvula. In the remaining species of *Spodoptera* the coremata can be either a single or in form of a double lobe. Character state tree - Fig. 13. *CI = 0.60.*

Juxta: *Character 18. Shape.* **(0)***(11):* hexagonal plate with dorsolateral arms (Fig. 101); **(1)** *(01):* helmet-shaped (Fig. 102); **(2)** *(33):* a narrow rectangular band with ventrolateral projections (Fig. 103); **(3)** *(32):* a rectangular band, median process elongate, expanding into an apical plate (Fig. 104); **(4)** *(21):* elliptical (Fig. 105); **(5)** *(31):* a narrow band, median process triangulate (Fig. 106); **(6)** *(30):* quadrate with lateral third distinct (Fig. 107); **(7)** *(41):* a narrow band expanded ventrolaterally, median projection broad, triangular (Fig. 108); **(8)** *(51):* a narrow band expanded ventrolaterally, median projection elongate, triangular (Fig. 109); **(9)** *(61):* a narrow band expanded ventrolaterally, median projection an elongate narrow triangle (Fig. 110). The juxta is a flat plate that joins the bases of the valves. Character state tree - Fig. 14. *CI = 0.90.*

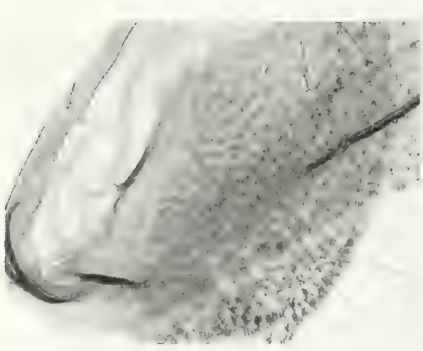
Vesica: *Character 19. Dorsobasal sclerotized patch.* **(0)***(110):* absent (Fig. 111); **(1)** *(220):* quadrate, gran-



Figs. 57–66. Ampullla: Character 10, form. 57, Elongate, sinuate process, apex pointed, state 0, *G. partita.* 58, Elongate process bent at a right angle at 2/3 length, state 1, *E. grata.* 59, Elongate, narrow, slightly curved, apex round, state 2, *S. exigua.* 60, Short, thumb-shaped lobe, apex round, state 3, *S. albula.* 61, Short, triangular shaped lobe, apex round, state 4, *S. ochrea.* 62, Minute lobe, state 5, *S. exempta.* 63, Elongate, slightly curved with a pointed produced apex, state 6, *S. cilium.* 64, Elongate, slightly curved with an angulate pointed apex, state 7, *S. apertura.* 65, Elongate, slightly curved with a decurved apex, state 8, *S. androgea.* 66, Elongate, broad, curved with a decurved apex, state 9, *S. latifascia.*



Figs. 67–76. Basal sclerite of clasper: Character 11, form. 67, Short, crescent-shaped, state 0, *G. partita.* 68, Oblique bar, state 1, *S. exigua.* 69, A narrow plate with an oblique bar at proximal end, state 2, *S. exempta.* 70, An elongate plate with costal and oblique bars joined to form a horizontal X, state 3, *S. apertura.* 71, A broad plate with an oblique bar at proximal end, state 4, *S. albula.* 72, A quadrate plate with slightly sclerotized costal bar and an elongate horizontal bar, state 5, *S. androgea.* 73, Plate reduced, costal and oblique bars form an obtuse angle, state 6, *S. frugiperda.* 74, An oblong plate, costal and oblique bars form an acute angle, state 7, *S. litura.* 75, A rectangular plate with costal and oblique bars joined to form a horizontal X, state 8, *S. pulchella.* 76, A reduced plate, costal bar curved and joining oblique bar to form an inverted Y, state 9, *S. cosmiodes.*



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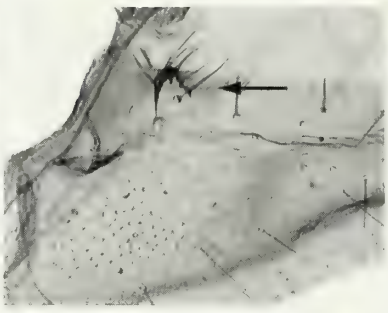

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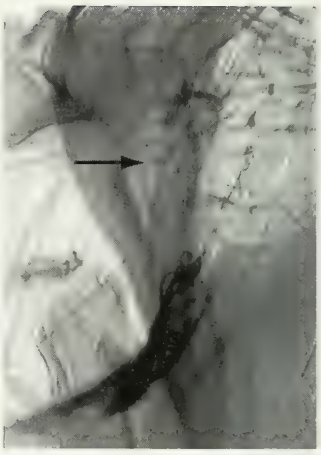

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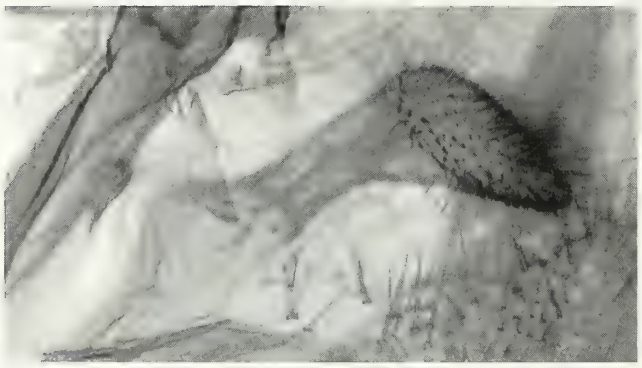

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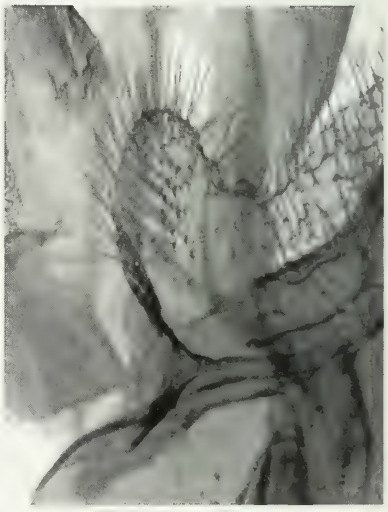

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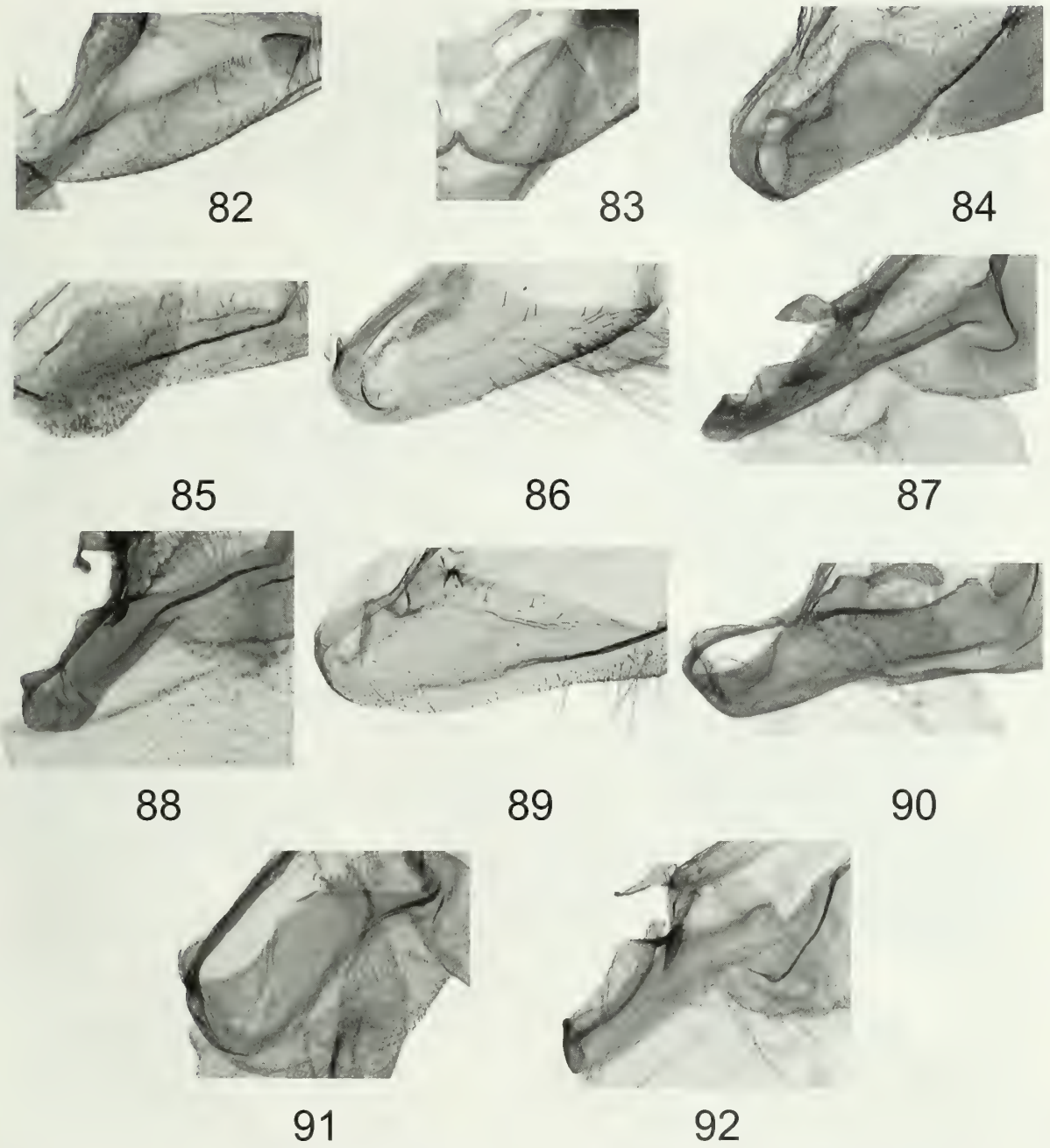
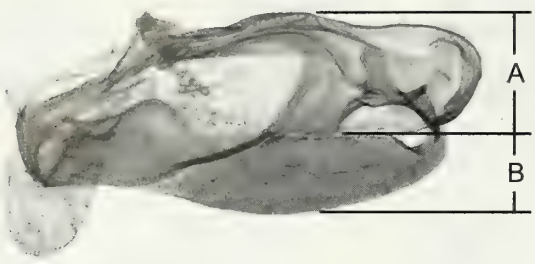
Figs. 77–81. Clavus: Character 12, shape. 77, Absent, state 1, *S. exigua.* 78, A minute round projection, state 2, *S. apertura.* 79, Elongate, finger-shaped, state 3, *S. dolichos.* 80, Large, club-shaped, base narrower than apex, state 4, *S. latifascia.* 81, Short, round, covered with setae, state 5, *S. ornithogalli.*

ulose (Fig. 112); **(2)** *(200):* single elongate spine (Fig. 113); **(3)** *(210):* narrow, elongate, aculeate (Fig. 114); **(4)** *(211):* dense patch of elongate spines (Fig. 115); **(5)** *(010):* narrow, elongate, granulose (Fig. 116); **(6)** *(310):* wide, elongate, aculeate (Fig. 117); **(7)** *(510):* narrow, elongate, granulose basally, aculeate apically (Fig. 118); **(8)** *(33):* quadrate, aculeate (Fig. 119). At the base of the vesica, where it emerges from the aedoeagus, is a variously shaped spiculate patch. The patch varies considerably from an indistinct patch with minute spiculations (Fig. 112) to a well developed spine (Fig. 113) or patch of large spines (Fig. 115). Character state tree - Fig. 15. *CI = 0.89.*

Character 20. Distal cornutus. **(0)***(01000):* conical (Fig. 120); **(1)** *(11000):* multiple conical cornuti (Fig. 121); **(2)** *(41000):* ovate, aculeate apically (Fig. 122); **(3)** *(31000):* absent (Fig. 123); **(4)** *(21000):* large spine (Fig. 124); **(5)** *(20000):* patch of large spines within dense cornutal patch (Fig. 125); **(6)**



Figs. 82–92. Sacculus: Character 13, shape. 82, Cylindrical with heavily scelerotized triangular apex, state 0, *G. partita.* 83, Quadrate, state 1, *E. grata.* 84, Broad to half its length, tapering distally, state 2, *S. albula.* 85, Rectangular, proximal margin wider than distal, state 3, *S. exigua.* 86, Trapezoidal, dorsal margin angulate, state 4, *S. cilium.* 87, Elongate, basal notch, widest at one-quarter length, gradually tapered to apex, state 5, *S. litura* . 88, Elongate, basal notch, widest at one-third length, abruptly tapered to apex, state 6, *S. pulchella.* 89,Triagulate, state 7, *S. apertura.* 90, Rectangular, slightly constricted at two-thirds length, apex indented, state 8, *S. cosmiodes.* 91, Quadrate, apex tapered distally, state 9, *S. androgea.* 92, Rectangular, apex truncate dorsally, an elongate taper ventrally, state 10, *S. dolichos.*



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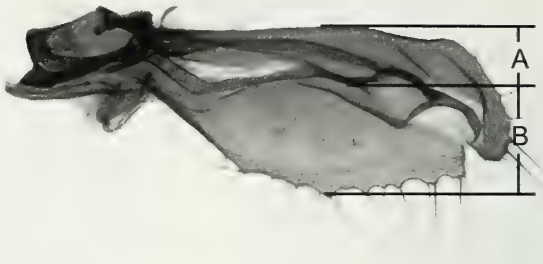
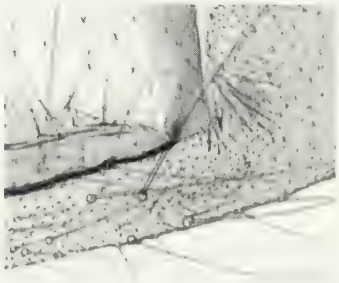
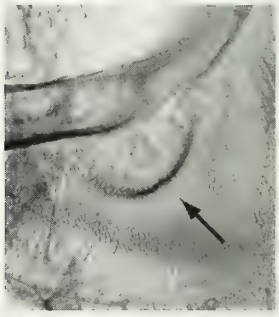


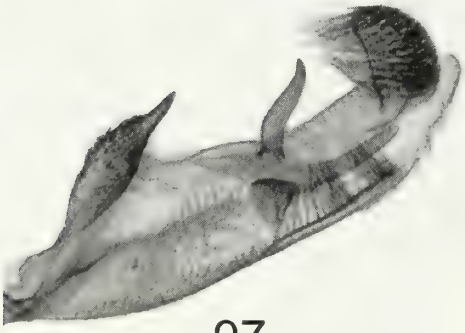
94



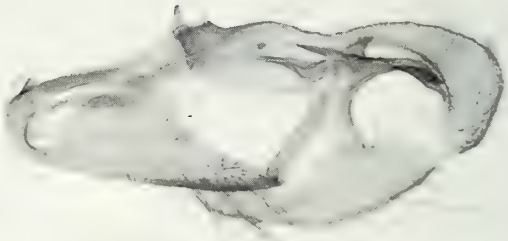
95



96



97



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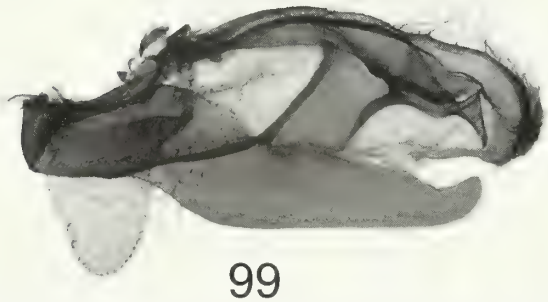

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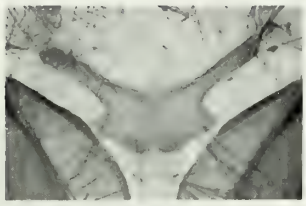
100

Figs. 93–96. Valvula characters. 93, Character 14: ventral margin shape: smooth, setae not originating on short protuberances, state 0; character 15: narrower than cucullus (A>B), state 0, *S. albula*. 94, Character 14: ventral magrin shape: scalloped, setae originating on short protuberances, state 1; character 15: wider than cucullus (A<B), state 1, *S. roseae*. 95, Character 16: Valvular indentation: absent, state 0, *S. exigua*. 96, Character 16: Valvular indentation: present, state 1, *S. frugiperda*. Figs. 97–100. Coremata: Character 17. Number of lobes. 97, Absent, state 0, *G. partita*. 98, No distinct lobe, appressed against sacculus, state 1, *S. cilium*. 99, Single lobe, state 2, *S. ochrea*. 100, Double lobe, state 3, *S. litura*.



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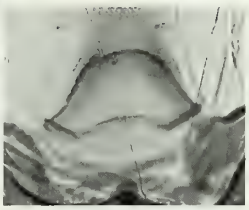
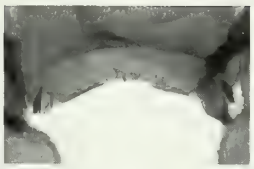


102



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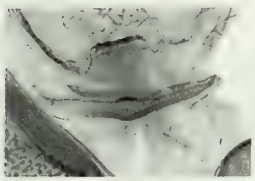
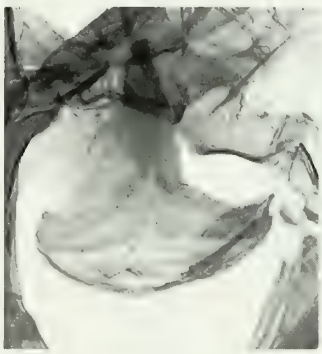
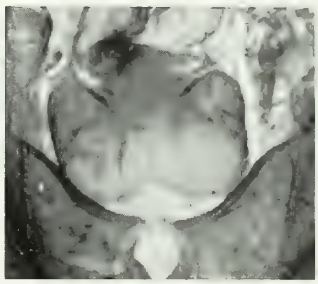


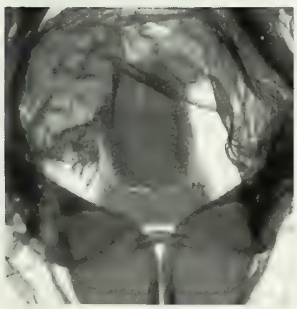
105



106



107



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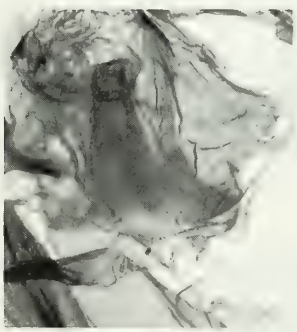

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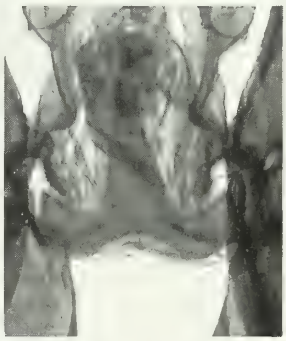
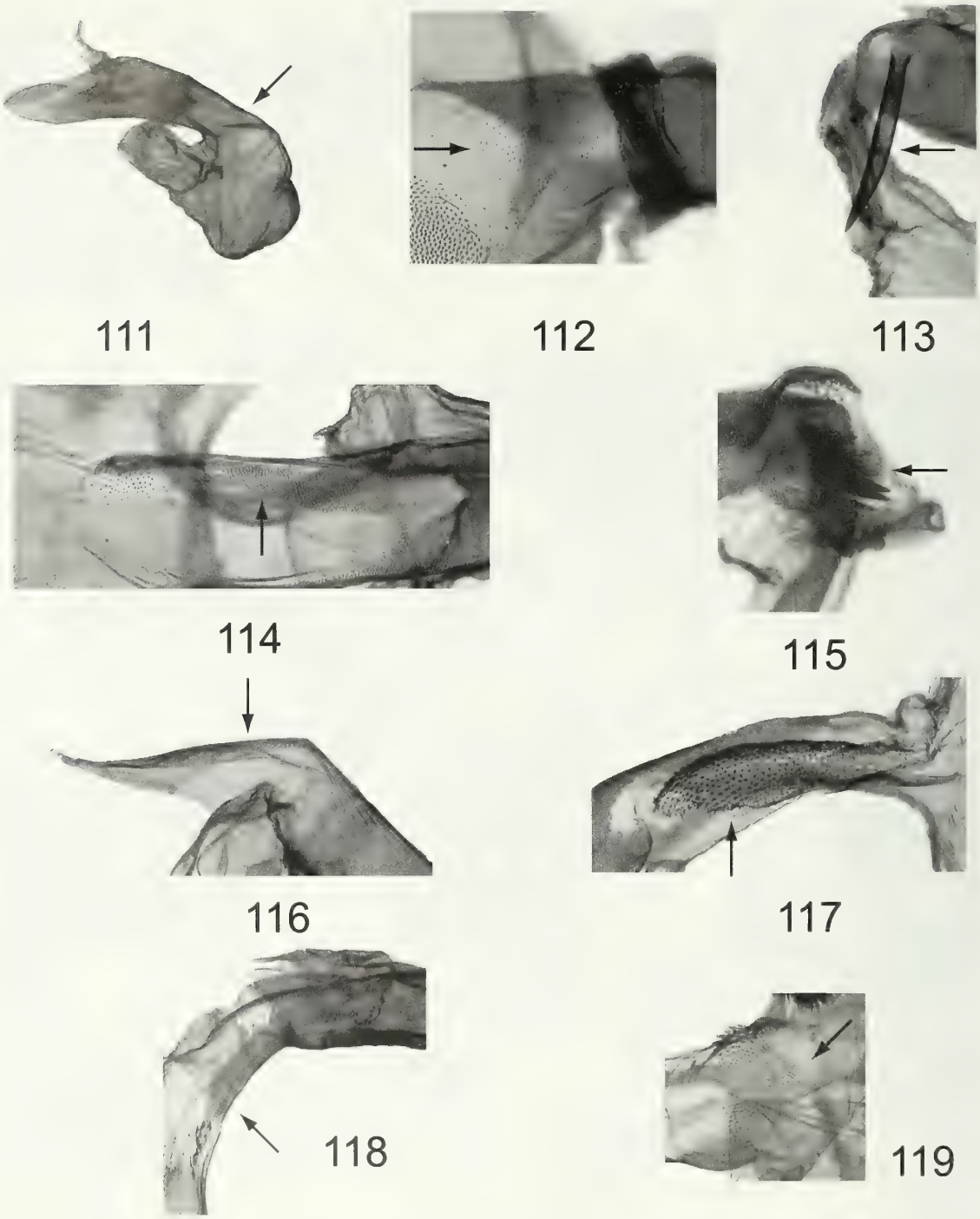


110

Figs. 101–110. Juxta: Character 18, shape. 101, Hexagonal plate with dorso-lateral arms, state 0, *E. grata.* 102, Helmet-shaped, state 1, *G. partita.* 103, A narrow rectangular band with ventro-lateral projections, state 2, *S. malagasy.* 104, A rectangular band, median process elongate, expanding into an apical plate, state 3, *S. pecten.* 105, Elliptical, state 4, *S. exigua.* 106, A narrow band, median process triangulate, state 5, *S. albula.* 107, Quadrate with lateral third distinct, state 6, *S. compta.* 108, A narrow band expanded ventro-laterally, median projection broad, triangular, state 7, *S. androgea.* 109, A narrow band expanded ventro-laterally, median projection elongate, triangular, state 8, *S. latifascia.* 110, A narrow band expanded ventro-laterally, median projection an elongate narrow triangle, state 9, *S. cosmiodes.*



Figs. 111–119. Vesica: Character 19, dorso-basal sclerotized patch.111, Absent, state 0, *G. partita.* 112, Quadrate, granulose, state 1, *S. apertura.* 113, Single elongate spine, state 2, *S. cilium.* 114, Narrow, elongate, aculeate, state 3, *S. frugiperda.* 115, Dense patch of elongate spines, state 4, *S. albula.* 116, Narrow, elongate, granulose, state 5, *S. exigua.* 117, Wide, elongate, aculeate, state 6, *S. picta.* 118, Narrow, elongate, granulose basally, aculeate apically, state 7, *S. descoinsi.* 119, Quadrate, aculeate, state 8, *S. pulchella.*

(21100): elongate sclerotized ribbon with aculeate apex (Fig. 126); **(7)** *(21010):* elongate sclerotized ribbon with apex spinulose (Fig. 127); **(8)** *(22000):* ovate, aculeate (Fig. 128); **(9)** *(23000):* a bulbous elliptical plate, apex aculeate (Fig. 129); **(10)** *(21001):* a bulbous elliptical plate, apex pointed (Fig. 130). The distal cornutus is a sclerotized patch or spine located distally on the vesica. It is absent in *S. umbraculata, cilium* clade, and clade 21. Character state tree - Fig. 16. *CI = 0.77.*

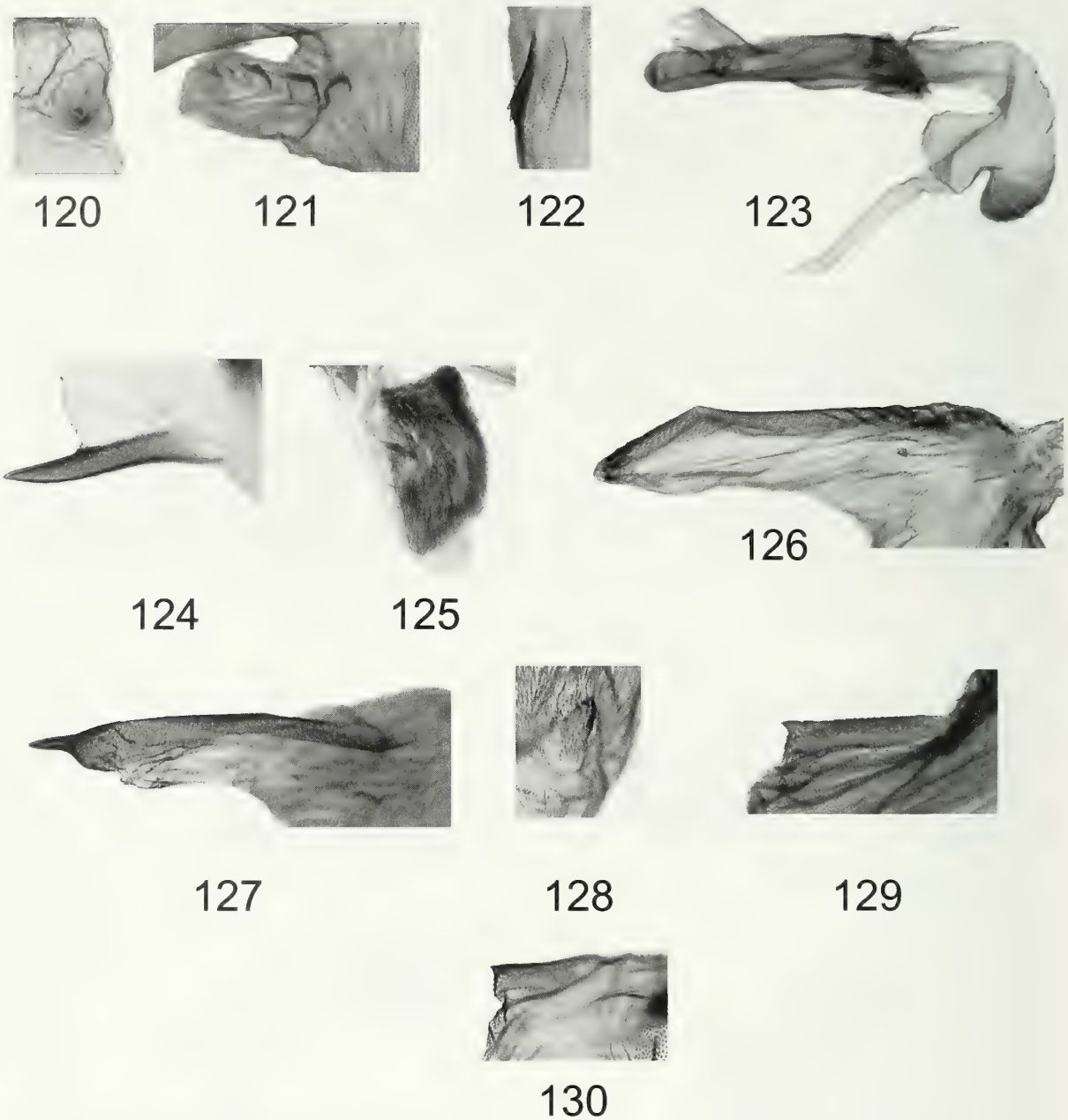
Character 21. Dense cornutal patch. **(0)***(0):* absent (Fig. 131); **(1)** *(1):* present (Fig. 132). The dense cornutal patch is present in all species of *Spodoptera.* It is a dense patch of fine hairs which are deciduous. If the hairs have been rubbed off, a patch of minute sockets can still be distinguished. *CI = 1.00.*

Character 22. Location of dense cornutal patch. **(0)***(00):* absent (Fig. 131); **(1)***(20):* mediodorsal on vesica (Fig. 132); **(2)** *(10):* apex of disto-lateral diverticulum (Fig. 133); **(3)** *(11):* apex of distal diverticulum (Fig. 134). The dense cornutal patch can be located on different areas of the vesica. Character state tree - Fig. 13. *CI = 0.50.*

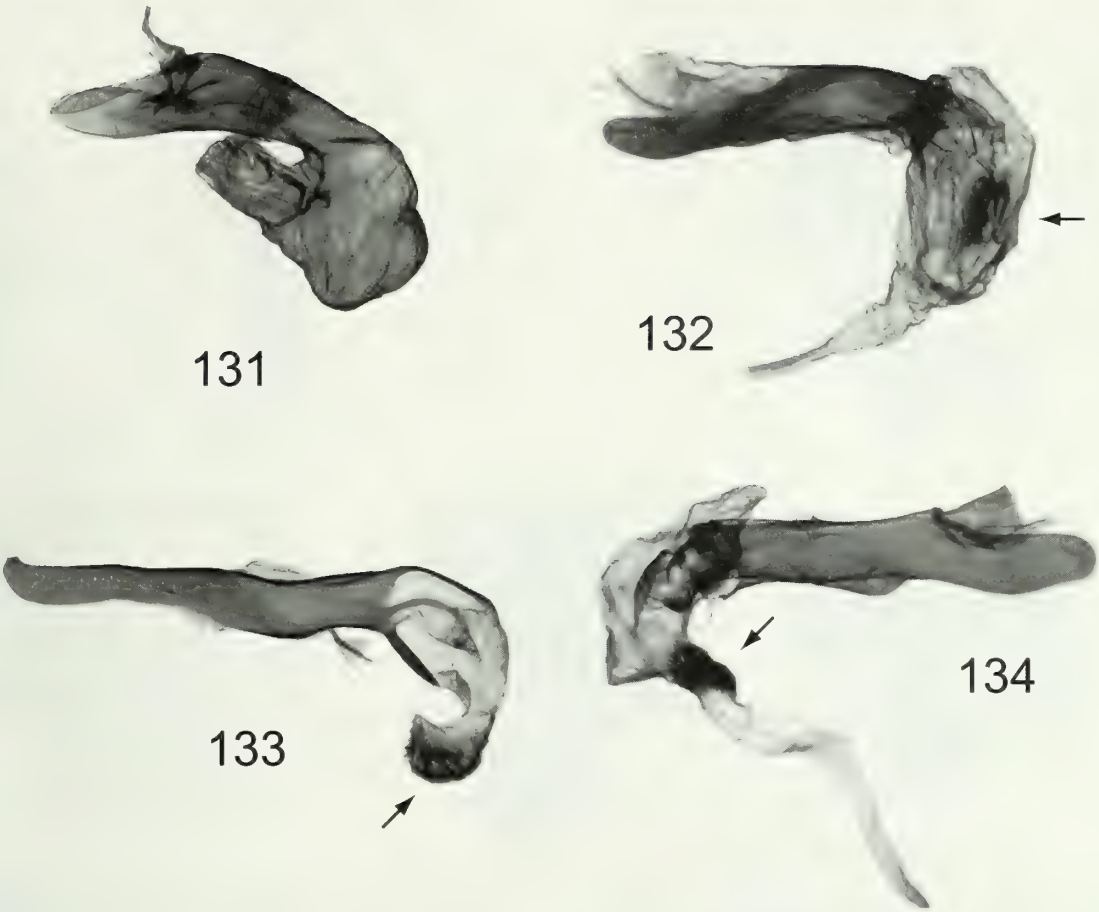
Female Genitalia

Ventral plate of ostium bursa: *Character 23. Form of distal margin.* **(0)***(1110):* straight (Fig. 135); **(1)** *(0110):* concave (Fig. 136); **(2)** *(1210):* convex (Fig. 137); **(3)** *(1010):* a long central groove leading into ductus bursae (Fig. 138); **(4)** *(1100):* a single median projection (Fig. 139); **(5)** *(2110):* U-shaped (Fig. 140); **(6)** *(2111):* a narrow U-shape (Fig. 141); **(7)** *(3110):* a wide rectangular notch (Fig. 142); **(8)** *(1120):* a broad V-shaped notch (Fig. 143). The ventral plate of the ostium bursa is variously modified and a good character to identify females of *Spodoptera.* Character state tree - Fig. 17. *CI = 1.00.*

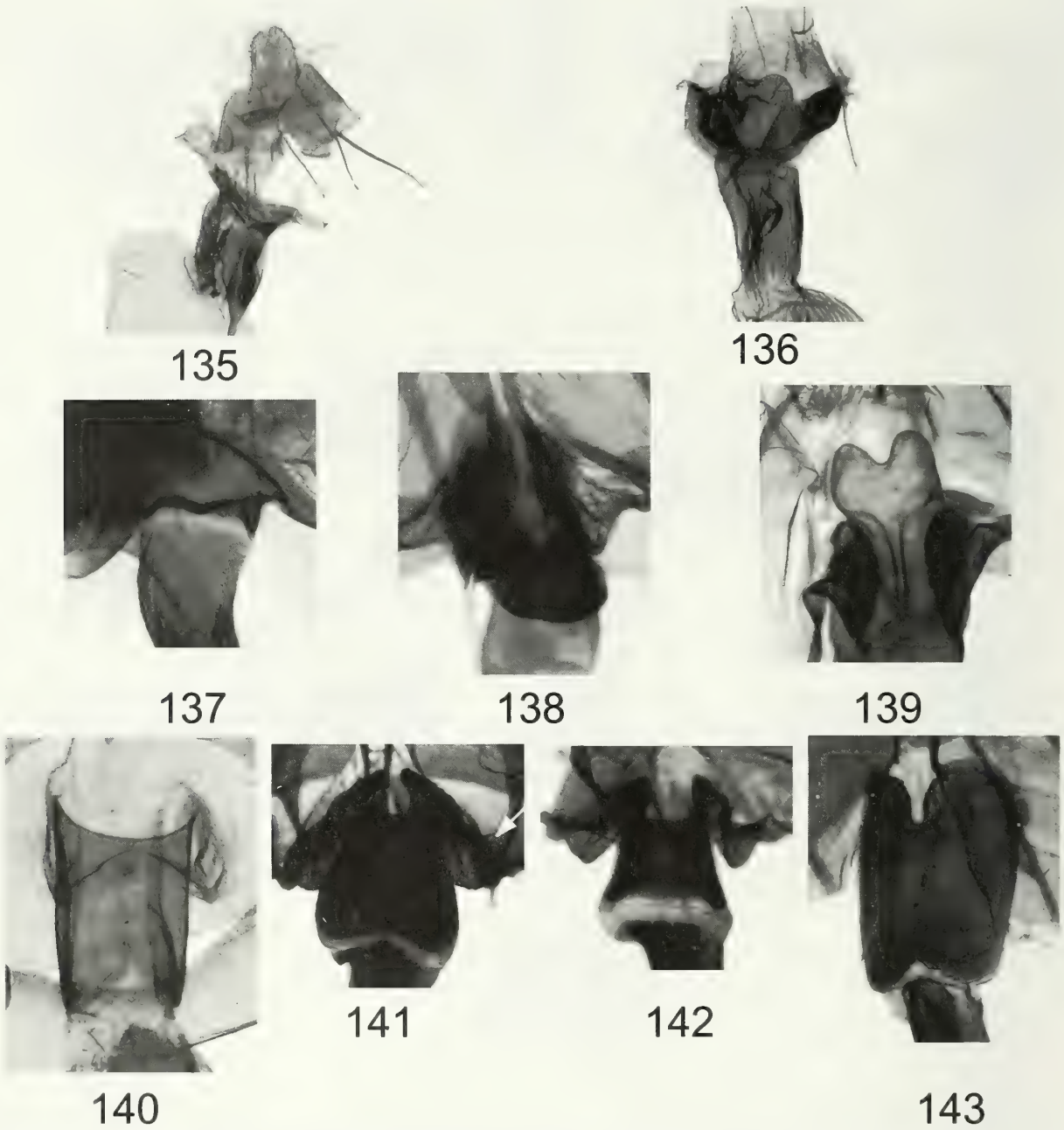
Character 24. Ventrolateral invaginated pocket of 8th sternite. **(0)***(0:* absent (Fig. 137); **(1)** *(1):* present (Fig. 139). Lateral to the ventral plate of the ostium bursa is an invaginated pocket. It is present in the *evanida* and *praefica* clades. *CI = 1.00.*



Figs. 120–130. Vesica: Character 20. Distal cornutus. 120, Conical, state 0, *E. grata.* 121, Multiple conical cornut, state 1, *G. partita.* 122, Ovate, aculeate apically, state 2, *S. apertura.* 123, Absent, state 3, *S. depravata.* 124, Large spine, state 4, *S. exigua.* 125, Patch of large spines within dense cornutal patch, state 5, *S. exempta.* 126, Elongate sclerotized ribbon with aculeate apex, state 6, *S. mauritia.* 127, Elongate sclerotized ribbon with apex spinulose, state 7, *S. triturata.* 128, Ovate, aculeate, state 8, *S. ornithogalli.* 129, A bulbous ellipitical plate, apex aculeate, state 9, *S. litura.* 130, A bulbous ellipitical plate, apex pointed, state 10, *S. descoinsi.*



Figs. 131–134. Vesica characters. 131, Character 21: dense cornutal patch: absent, state 0; character 22: location of dense cornutal patch: absent, state 0, *G. partita.* 132, Character 21: dense cornutal patch: present, state 1; character 22: location of dense cornutal patch: medio-dorsal on vesica, state 1, *S. malagasy.* 133, Character 22: location of dense cornutal patch: Apex of disto-lateral diverticulum, state 2, *S. cilium.* 134, Character 22: location of dense cornutal patch: apex of distal diverticulum, state 3, *S. dolichos.*



Figs. 135–143. Ventral plate of ostium bursa: Character 23, form of distal margin. 135, Straight, state 0, *E. grata.* 136, Concave, state 1, *G. partita.* 137, Convex, state 2; character 24: ventrolateral invaginated pocket of 8th sternite: absent, state 0, *S. exempta.* 138, A long central groove leading into ductus bursae, state 3, *S. cilium.* 139, A single median projection, state 4, *S. eridania.* 140, U-shaped, state 5, *S. roseae.* 141, A narrow U-shape, state 6; character 24: ventrolateral invaginated pocket of 8th sternite: present, state 1, *S. cosmiodes.* 142, A wide rectangular notch, state 7, *S. latifascia.* 143, A broad V-shaped notch, state 8, *S. litura.*

ADULT SYSTEMATIC TREATMENT

Checklist

The following is a checklist of *Spodoptera* arranged alphabetically. The valid species are in bold with synonyms in italics. The name in parentheses after each species is the original genus in which the specific name was described. An asterisk after a species name means that the type was examined during this study.

Spodoptera Guenée 1852
Laphygma Guenée 1852
Prodenia Guenée 1852
Calogramma Guenée 1852
Rusidrina Staudinger 1892
Douzdrina de Laever 1985
albula* (Walker, 1857b) (*Xylina*)
*orbicularis** (Walker, 1857b) (*Laphygma*)
*caudata** (Walker, 1869) (*Laphygma*)
androgea (Stoll *in* Cramer, 1782) (*Phalaena Noctua*)
*rubrifusa** (Hampson, 1909) (*Prodenia*)
apertura (Walker, 1865) (*Prodenia*)
*synstictis** (Hampson, 1896) (*Prodenia*)
*leucophlebia** (Hampson, 1902) (*Prodenia*)
*connexa** (Wileman, 1914) (*Laphygma*) **New synonym.**
*teferii** Laporte *in* Rougeot, 1984 (*Spodoptera*) **New synonym.**
cilium Guenée 1852 (*Spodoptera*)
cycloides (Guenée, 1852) (*Laphygma*)
capicola Herrich-Schäffer, [1854] (*Spodoptera*)
latebrosa (Lederer, 1855) (*Caradrina*)
*insignata** (Walker, 1857a) (*Caradrina*)
*orbicularis** (Walker, 1857a) (*Caradrina*)
*praeterita** (Walker, 1857a) (*Caradrina*)
*procedens** (Walker, 1857b) (*Laphygma*)
obliterans (Walker, 1862b) (*Laphygma*)
imperviata (Walker, 1865a) (*Laphygma*)
retrahens (Walker, 1870) (*Laphygma*)
compta* (Walker, 1869) (*Laphygma*)
cosmiodes* (Walker, 1858) (*Prodenia*)
depravata* (Butler, 1879) (*Agrotis*)
inutilis (Alpheraky, 1897) (*Luperina*)
rasdolnia (Staudinger, 1892) (*Rusidrina*)
kaolina (Bryk, 1949) (*Euxoa*)
descoinsi Lalanne-Cassou & Silvain, 1994 (*Spodoptera*)
dolichos (Fabricius, 1794) (*Noctua*)
commelinae (J.E. Smith, 1797) (*Phalaena*)
marmorea (Sepp, [1840]) (*Phalaena*)
eridania (Stoll *in* Cramer 1782) (*Phalaena*)
linea (Fabricius, 1794) (*Noctua*)
phytolaccae (J.E. Smith, 1797) (*Phalaena*)
*putrida** (Guenée, 1852) (*Xylomyges*)
*amygia** (Guenée, 1852) (*Xylomyges*)
*externa** (Walker, 1856) (*Leucania*)
bipunctata (Walker, 1857b) (*Xylina*)
*inquieta** (Walker, 1857b) (*Xylina*)
*strigifera** (Walker, 1858) (*Prodenia*)
*peruviana** (Walker, 1865a) (*Laphygma*)
*communicata** (Walker, 1869) (*Laphygma*)
derupta (Morrison, 1875) (*Actinotia*)
*ignobilis** (Butler, 1878) (*Prodenia*)
nigrofasciata (Hulst, 1881) (*Leucania*)
recondita (Möschler, 1890) (*Callierges*)
evanida* Schaus, 1914 (*Spodoptera*)
exempta* (Walker, 1857a) (*Agrotis*)
*bipars** (Walker, 1857b) (*Prodenia*)
*ingloria** (Walker, 1858) (*Prodenia*)
*metriodes** (Bethune-Baker, 1911) (*Prodenia*) **New synonym.**
exigua (Hübner, 1808) (*Noctua*)
fulgens (Geyer, 1832) (*Noctua*)
pygmaea (Rambur, 1834) (*Caradrina*)
*junceti** (Zeller, 1847) (*Caradrina*)
*caradrinoides** (Walker, 1856) (*Laphygma*)
*flavimaculata** (Harvey, 1876) (*Caradrina*)
sebghana (Austaut, 1880) (*Caradrina*)
*venosa** (Butler, 1880a) (*Caradrina*)
flavimaculata (Smith, 1893) (*Laphygma*)
*antipodea** (Warren *in* Seitz, 1914a) (*Laphygma*)
frugiperda (J.E. Smith, 1797) (*Phalaena*)
*macra** (Guenée, 1852) (*Laphygma*)
*inepta** (Walker, 1856) (*Laphygma*)
*signifera** (Walker, 1856) (*Prodenia*)
*plagiata** (Walker, 1856) (*Prodenia*)
*autumnalis** (Riley, 1871) (*Prodenia*)
latifascia (Walker, 1856) (*Prodenia*)
*variolosa** (Walker, 1857b) (*Prodenia*)
littoralis (Boisduval, 1833) (*Hadena*)
retina (Freyer, 1845) (*Hadena*)
testaceoides (Guenée, 1852) (*Prodenia*)
litura (Fabricius, 1775) (*Noctua*)
histrionica (Fabricius, 1775) (*Noctua*)
elata (Fabricius, 1781) (*Noctua*)
tasmanica (Guenée, 1852) (*Prodenia*)
*ciligera** (Guenée, 1852) (*Prodenia*)
*subterminalis** (Walker, 1856) (*Prodenia*)
*glaucistriga** (Walker, 1856) (*Prodenia*)
*declinata** (Walker, 1857b) (*Prodenia*)
albisparsa (Walker, 1862) (*Mamestra*)
*evanescens** (Butler, 1884) (*Prodenia*)
malagasy* Viette, 1967 (*Spodoptera*)
marima* (Schaus, 1904) (*Prodenia*)
mauritia (Boisduval, 1833) (*Hadena*)
acronyctoides Guenée, 1852a (*Spodoptera*)
acronyctiformis Guenée, 1852b (*Spodoptera*)
*filum** Guenée, 1852a (*Spodoptera*)
*nubes** Guenée, 1852a (*Spodoptera*)
*infecta** (Walker, 1856) (*Prodenia*)
insignata (Walker, 1856) (*Prodenia*)
*transducta** (Walker, 1857a) (*Agrotis*)
*permunda** (Walker, 1857b) (*Prodenia*)

*aliena** (Walker, 1865a) (*Agrotis*)
*bisignata** (Walker, 1865a) (*Agrotis*)
*squalida** (Walker, 1865a) (*Laphygma*)
*venustula** (Walker, 1865a) (*Prodenia*)
*submarginalis** (Walker, 1865a) (*Agrotis*)
*obliqua** (Walker, 1865b) (*Hadena*)
formosana (Matsumura *in* Shiraki, 1913) (*Hermonassa*)
ogasawarensis (Matsumura, 1926) (*Euxoa*)
ochrea* (Hampson, 1909) (*Xylomyges*)
ornithogalli* (Guenée, 1852a) (*Prodenia*)
eudiopta (Guenée, 1852a) (*Prodenia*)
*flavimedia** (Harvey, 1875) (*Prodenia*)
*lineatella** (Harvey, 1875) (*Prodenia*)
praefica form *eudioptoides** (Barnes & Benjamin, 1923) (*Prodenia*)
pecten* Guenée, 1852a (*Spodoptera*)
*infixa** (Walker, 1862a) (*Agrotis*) **New synonym.**
*insulsa** Walker, 1865 (*Spodoptera*) **New synonym.**
*erica** Butler, 1880b (*Spodoptera*)
*uniformis** (Swinhoe, 1890) (*Spaelotis*)
*pectinata** (Hampson, 1894) (*Caradrina*)
*speciosa** (Rothschild, 1920) (*Elydna*)
pectinicornis* (Hampson, 1895) (*Xanthoptera*)
*hennia** (Swinhoe, 1901) (*Caradrina*)
picta (Guérin-Méneville, 1838) (*Polia*)
festiva (Donovan, 1805) (*Phalaena*)
praefica* (Grote, 1875) (*Prodenia*)
pulchella (Herrich-Schäffer, 1868) (*Laphygma*)
exquisita (Möschler, 1886) (*Prodenia*)
roseae* (Schaus, 1923b) (*Trachaea* [sic])
triturata* (Walker, 1857a) (*Caradrina*)
*gratiosa** (Walker, 1865a) (*Laphygma*)
*bisignata** (Walker, 1865a) (*Celaena*)
umbraculata* (Walker, 1858) (*Eumichtis?*)
enunciatus (Lucas, 1892) (*Agrotis*)
*andrias** (Meyrick, 1902) (*Hadena*)

Spodoptera Guenée

Spodoptera Guenée 1852a: 153 [type species: *Hadena mauritia* Boisduval by subsequent designation by Hampson 1894: 248]; Walker 1856: 185; Cotes & Swinhoe 1888: 325; Hampson 1894: 248, 1909: 251; Turner 1920: 146; Zimmerman 1958: 331; Boursin 1964: 238; Viette 1967: 519; Forster & Wohlfahrt 1971: 159; Franclemont & Todd 1983: 141; Goater 1983: 275; Poole 1989: 922; Holloway 1989: 132; Edwards 1996: 324; Poole & Gentili 1996: 773; Kononenko *et al.* 1998: 233.

Laphygma Guenée 1852a: 156 [type species: *Noctua exigua* Hübner by original designation]; Walker 1856: 187; Druce 1889: 267; Smith 1893: 168; Grote 1895: 42; Dyar 1903 ["1902"]: 123; Hampson 1909: 258; Barnes & McDunnough 1917: 67; Turner 1920: 146 [jr. synonym of *Spodoptera*]; McDunnough 1938: 96; Poole 1989: 567.

Prodenia Guenée 1852a: 159 [type species: *Hadena retina* Feyer by subsequent designation by Grote 1874: 17]; Walker 1856: 191; Cotes & Swinhoe 1888: 326; Druce 1889: 268; Smith 1893: 169; Hampson 1894: 247, 1909: 240; Grote 1895: 42; Dyar 1903: 123; Barnes & McDunnough 1917: 67; Turner 1920: 146; McDunnough 1938: 96; Viette 1963: 146 [jr. synonym of *Spodoptera*]; Chen *et al.* 1991: 230; Poole 1989: 834.

Calogramma Guenée 1852a: 165 [type species: *Polia picta* Guérin-Méneville by monotypy]; Walker 1856: 198; Hampson 1894: 249, 1909: 238; Turner 1920: 146; Sugi 1982: 763 [jr. synonym of *Spodoptera*]; Poole 1989: 192.

Rusidrina Staudinger 1892: 491 [type species: *Rusidrina rasdolnia* by monotypy]; Poole 1989: 885.

Douzdrina de Laever 1985: 148 [type species: *Douzdrina protector* de Laever by monotypy]; Yela 1985 ["1984"]: 212 [junior synonym of *Spodoptera*].

Diagnosis.—*Spodoptera* species can be recognized by the gray to brown forewing ground color and white hindwing. Several forewing patterns exist and once recognized can distinguish *Spodoptera* from other genera (Figs. 172, 181, 221, 235, 259, 268). An exception to the forewing ground color is found in *S. picta* (Guérin-Méneville) which has a cream colored forewing with irregular patches of rose scales (Fig. 278). In the male genitalia the valvula is separate from the valve apically, except in *S. exigua*. The females have a large tuft of dense scales encircling the eighth abdominal segment.

Description.—*Head (Fig. 170:* Vestiture smooth. Eye and ocellus well developed. Labial palpus appressed to front; scales smooth; length of basal segment 0.59–0.82 times length of median segment; length of apical segment 0.37–0.67 times length of median segment. Scape scaled, smooth. Antenna filiform, bipectinate, or serrate in male; filiform in female; scaled dorsally. Pilifers present. Haustellum well developed.

Thorax: Scales smooth. Prothoracic leg with epiphysis 0.38–0.55 times length of tibia; tibia lacking spines. Mesothoracic tibia lacking spines; pair of unequal sized apical spurs, in male of most species an unscaled area present on apical spurs. Metathoracic tibia lacking spines; two pair of unequal sized apical spurs; basal spurs originating at 0.5–0.6 length of tibia.

Forewing (Fig. 171): Male length, 8–22 mm; female length 8.3–22 mm. Length of wing 2.05–2.85 times width. Veins Sc, R1, R2, and R3 reaching costal margin, R4 to apex, R5 to termen; R3 and R4 forked at 0.1–0.3 beyond accessory cell; R5 originates from apex of accessory cell. M3 and CuA1 separate. CuA2 originates beyond 0.65 length of discal cell.

Hindwing: Male with a single frenulum; female with three frenula. Vein Sc + R1 greater than 0.9 wing length. M2 vestigial, represented by a faint fold.

Abdomen: Dorsal scale tuft on segment one large and conspicuous, smaller dorsal tufts on segments 2 and 3 (fresh specimens). Female with fine dense scales on eighth segment.

Male Genitalia: Uncus curved. Clasper well developed. Valvula with a distinct apex and separate from cucullus (except in *S. exigua*). Coremata present, usually well developed into elongate lobes.

Female Genitalia: Eighth segment well developed. Ventral plate of ostium bursae sclerotized. Accessory bursa present. Signum present.

Keys to Species

The species of *Spodoptera* can conveniently be divided into New and Old World faunas. The only species that is distributed worldwide is *S. exigua.* Most species can be identified easily. The problem areas are separating *S. littoralis* and *S. litura* in the Old World, and *S. descoinsi, S. cosmiodes,* and *S. latifascia* in the New World. All of these species can be separated by using both male and female genitalia. Species identifications can usually be resolved by their geographic distributions. *Spodoptera littoralis* is distributed in Europe, the Middle East, and Africa, whereas *S. litura* is distributed in Asia, Australasia, and Oceania. *Spodoptera descoinsi* is known only from French Guiana and Peru, *S. cosmiodes* is South American in distribution, and *S. latifascia* ranges from the southern United States to Panama and the Caribbean.

Additional keys to adults have been published for the faunas of Africa (Brown & Dewhurst 1975), the Western Hemisphere (Todd & Poole 1980), and Florida (Heppner 1998).

KEY TO ADULTS OF OLD WORLD SPECIES

1. Antenna serrate (Fig. 20) 2
1′. Antenna bipectinate (Fig. 19) 4
1″. Antenna filiform (Fig. 18) 7
2(1). Forewing with orbicular spot an oblique rectangle, cream with a brown center, bordered by thin black lines; white scales along Cu vein under orbicular and reniform spots extending to M3 and Cu1 veins (Figs. 212–218) 3
2′. Forewing with orbicular spot round, cream, with buff to brown center, outlined in black (can be completely cream); no white scales along Cu vein under orbicular and reniform spots (Figs. 181, 183, 186, 189) ..... *S. cilium* Guenée ♂
3(2). Forewing ground color dark brown; hindwing ground color white (Figs. 212–215); Ethiopian, Oriental, and Australasian (Fig. 527) ..... *S. apertura* (Walker) ♂
3′. Forewing ground color brown; hindwing ground color brown (Figs. 216–217); endemic to Madagascar (Fig. 528) ..... *S. malagasy* Viette ♂
4(1′). Forewing with orbicular spot cream, lacking rufous scales (Figs. 190–192, 194–195, 197, 199, 201, 204–205); length greater than 10 mm 5
4′. Forewing with orbicular spot indistinct, with rufous scales (Figs. 207–209, 211); length 8–8.3 mm ..... *S. pectinicornis* (Hampson) ♂
5(4). Hindwing white with wide suffused brown border (Figs. 190–192, 204–205) 6
5′. Hindwing white with narrow light brown border that can be almost absent (Figs. 194–195, 197, 199, 201) ..... *S. pecten* Guenée ♂
6(5). Patagium light brown with a median brown transverse band (Figs. 190–192); China, Korea, Japan (Fig. 524) ..... *S. depravata* (Butler) ♂
6′. Patagium banded, basal band rufous mixed with black or completely black, a thin black row of scales separating white median band, distal band light brown (Figs. 204–205); Australia (Fig. 526) ..... *S. umbraculata* (Walker) ♂
7(1″). Prothoracic tibia with lateral scale tufts extending beyond first tarsal segment (Fig. 22) 8
7′. Prothoracic tibia with lateral scale tufts shorter than first tarsal segment (Fig. 21) 9
8(7). Prothoracic tibia with lateral scale tufts extending beyond third tarsal segment; widely distributed in the Old World tropics from coastal Africa, India, Asia, Australia, Papua New Guinea and the Pacific islands west to Hawaii (Fig. 532) ..... *S. mauritia* (Boisduval) ♂

8′. Prothoracic tibia with lateral scale tufts extending beyond first tarsal segment; hindwing with thin margin of light brown scales, veins white, not infuscated with light brown scales (Figs. 249, 251); endemic to sub-Saharan Africa (Fig. 533) ..... *S. triturata* (Walker) ♂

9(8). Forewing ground color cream with an irregular patch of rose scales from oblique ground color band to postmedian line between costa and R vein (Fig. 278); forewing length 18–22 mm; Oriental, Australasian, and Oceania (Fig. 538) ..... *S. picta* (Guérin-Méneville) ♂ ♀

9′. Forewing ground color not cream and no rose scales present 10

10(9′). Forewing length greater than 10 mm 11

10′. Forewing length less than 10 mm ..... *S. pectinicornis* (Hampson) ♀

11(10). Forewing with orbicular spot round (Figs. 172–180, 182, 184–185, 187–188, 206) 12

11′. Forewing with orbicular spot oval or absent (Figs. 193, 196, 198, 200, 202–203, 230–234, 236–240, 246–247, 250, 252) 14

11″. Forewing with orbicular spot an oblique trapezoid that extends from costal margin to Cu vein (Figs. 212, 218, 263–267, 268–277) 18

12(11). Hindwing with apex, outer margin, and veins infuscated with light brown scales (Figs. 172–180, 206) 13

12′. Hindwing with gray scales along apex and outer margin, veins not infuscated with gray scales (Figs. 182, 184–185, 187–188) ..... *S. cilium* Guenée ♀

13(12). Forewing orbicular spot large, cream, no contrasting color in center, faintly outlined in black; length greater than 15 mm (Fig. 206) ..... *S. umbraculata* (Walker) ♀

13′. Forewing orbicular spot small, cream, center buff, not outlined in black; length less than 15 mm (Figs. 172–180) ..... *S. exigua* (Hübner) ♂ ♀

14(11′). Mesothoracic tarsus fuscous with cream colored apical rings 15

14′. Mesothoracic tarsus cream colored 17

15(14). Hindwings with veins infuscated with brown to base (Figs. 230–234, 236–240, 246–247) 16

15′. Hindwings with veins infuscated with brown at apex, white to base (Figs. 250, 252) ..... *S. triturata* (Walker) ♀

16(15). Forewing orbicular spot distinct, with buff to brown center, in some specimens outlined in black; reniform spot dark surrounded by a white to cream ring and an outer black ring (Figs. 230–234) ..... *S. exempta* (Walker) ♂ ♀

16′. Forewing orbicular spot faint to absent, never outlined in black; reniform spot black, lacking any border (Figs. 236–240, 246–247) ..... *S. mauritia* ♀

17(13′). Forewing with very faint wing markings, antemedial and postmedial lines absent, orbicular spot very faint to absent, reniform spot round, black and faint; hindwing white with apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales (Figs. 196, 198, 200, 202–203) ..... *S. pecten* Guenée ♀

17′. Forewing with wing markings present; hindwing white suffused with pale gray (Fig. 193) ..... *S. depravata* (Butler) ♀

18(11″). Forewing with reniform spot brown outlined in white on proximal border, distal apex with a triangular light brown spot outlined in white, a white distal border extending to middle (Figs. 263–277) 19

18′. Forewing with reniform spot crescent-shaped, lacking light brown triangular spot outlined in white at apex (Figs. 212, 218) 20

19(18′). Hindwing veins infuscated with brown scales apically (Figs. 268–277); Oriental, Australasia, and eastern Palaearctic regions (Fig. 537) ..... *S. litura* (Fabricius) ♂ ♀

19′. Hindwing veins not infuscated with brown scales near apex (Figs. 263–267); western Palaearctic and Ethiopian regions (Fig. 537) ..... *S. littoralis* (Boisduval) ♂ ♀

20(18′). Forewing ground color dark brown, reniform spot cream outlined in black, center light brown to brown; hindwing white (Fig. 212) ..... *S. apertura* (Walker) ♀

20′. Forewing ground color brown, reniform spot cream outlined in black, center light brown with a white median line; hindwing light brown (Fig. 218); endemic to Madagascar (Fig. 528) .*S. malagasy* Viette ♀

KEY TO ADULTS OF NEW WORLD SPECIES

1. Antenna serrate (Fig. 20); endemic to the Galapagos Islands (Fig. 543) ..... *S. roseae* (Schaus) ♂

1′. Antenna filiform (Fig. 18) 2

2(1′). Forewing orbicular spot round (Figs. 172–180, 303) 3

2′. Forewing with orbicular spot oval (Figs. 222, 225, 227–228) or an oblique trapezoid extending from costal margin to Cu vein (Figs. 259, 261, 284, 286–287, 290–291, 293, 296, 300) 4

3(2). Forewing with orbicular spot cream, with pale rufous center; forewing length 11–14 mm (Figs. 172–180) ..... *S. exigua* (Hübner) ♂ ♀

3′. Forewing with orbicular spot cream, with buff to brown center, outlined in black; forewing length 20–22 mm (Fig. 303); endemic to the Galapagos Islands (Fig. 543) ..... *S. roseae* (Schaus) ♀

4(2′). Forewing with no white scales along Cu vein under orbicular and reniform spots (Figs. 219–229, 253–258, 279–290) 5

4′. Forewing with white scales along Cu vein under orbicular and reniform spots extending to M3 and Cu1 veins, continuing down CuA2 vein to postmedial line (Figs. 259–262, 291–300) 13

5(4). Forewing ground color rufous (Figs. 219–223, 283, 285–290) 6

5′. Forewing ground color pale gray or cream (Figs. 224–229, 279–281) 9

5″. Forewing ground color brown, or dark brown (Figs. 253–258, 282, 284) 11

6(5). Forewing with costal and posterior margin areas concolorous (Figs. 219–220, 279–281, 285–286) 7

6′. Forewing with costal area darker than posterior marginal area (Figs. 283, 287–290) 16

7(5). Forewing with a distinct pale gray postmedian band between subterminal and adterminal lines (Figs. 285–286) ..... *S. cosmiodes* (Walker) ♂

7′. Forewing lacking a distinct postmedian band between subterminal and adterminal lines (Figs. 219–220, 279–281) 8

8(7′). Forewing lacking spots and lines, subterminal line faint, extending from outer margin to vein M1 (Figs. 219–220); rare, known only from Peru ..... *S. compta* (Walker) ♂ ♀

8′. Forewing with orbicular and reniform spots, antemedial and postmedial lines present, but faint, subterminal line faint (Figs. 279–281); uncommon, northcentral South America including Colombia, Venezuela, French Guiana, and northern Brazil (Fig. 539) ..... *S. evanida* Schaus ♂ ♀

9(5′). Forewing with a narrow, black longitudinal dash at base of Cu vein (Figs. 224–226); southern United States to northern Argentina and southern Brazil (Fig. 530) ..... *S. albula* (Walker) ♂ ♀

9′. Forewing lacking a narrow, black longitudinal dash at base of Cu vein (Figs. 221–223, 227–229) 10

10(9′). Hindwing with some contrasting scales along margin (Figs. 221–223); forewing of some specimens with a distinct broad longitudinal black streak from apex of discal cell to margin (Fig. 223); southern United States to Argentina (Fig. 529) ..... *S. eridania* (Stoll) ♂ ♀

10′. Hindwing with no contrasting scales along margin, completely white; never with a distinct broad longitudinal black streak from apex of discal cell to margin (Figs. 227–229); western Peru and Ecuador (Fig. 530) ..... *S. ochrea* (Hampson) ♂ ♀

11(5″). Forewing with a rufous area between antemedial and postmedial lines ventral to Cu and CuA2 veins that extends to outer margin (Figs. 282, 284) ..... *S. latifascia* (Walker) ♂

11′. Forewing lacking a rufous area between antemedial and postmedial lines ventral to Cu and CuA2 veins that extends to outer margin (Figs. 253–258) 12

12(11′). Forewing ground color brown with contrasting markings, a small conspicuous white spot at junction of M3 and CuA1 veins, and a white patch at apex (Figs. 253, 257) ..... *S. frugiperda* (J.E. Smith) ♂

12′. Forewing ground color dark brown without contrasting markings (Figs. 254–256, 258) ..... *S. frugiperda* (J.E. Smith) ♀

13(4′). Forewing with white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 continuing down CuA2 vein to postmedial line only, no white scales along veins M3 and CuA1 (a few scales present but not reaching postmedial line) (Figs. 259–262, 290) 14

13′. Forewing with white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 continuing down veins M3, CuA1, and CuA2 to postmedial line (Figs. 291–300) 18

14(13). Forewing orbicular spot small, not reaching costa (Figs. 259–262) 15

14′. Forewing orbicular spot large, reaching from Cu vein to costa (Fig. 290) ..... *S. descoinsi* Lalanne-Cassou & Silvain ♂

15(14). Tegula with a black and brown stripe along lateral margin (Fig. 259) ..... *S. dolichos* (Fabricius) ♂ ♀

15′. Tegula pale rufous to light brown, no stripes along lateral margin (Figs. 260–262) *S. androgea* (Stoll) ♂ ♀

16(6′). Hindwing margin with few scales along outer margin, not extending past CuA2 vein, a few scales at apex of Rs vein (Figs. 287–290) 17

16′. Hindwing margin with a wider border of scales than above that extends past CuA2 vein, scales on apices of veins Rs to CuA2 (Fig. 283) ..... *S. latifascia* (Walker) ♀

17(16). Shortest of the meso- and metathoracic tibial spurs with more cream than fuscous; meso- and metatho-

racic tarsi more fuscous than rufous (Figs. 287–289); common, widespread throughout South America (Fig. 540) ..... *S. cosmiodes* (Walker) ♀

17′. Shortest of the meso- and metathoracic tibial spurs with more fuscous than cream; meso- and metathoracic tarsi more rufous than fuscous (Fig. 290); uncommon, known only from French Guiana and Peru (Fig. 540) ..... *S. descoinsi* Lalanne-Cassou & Silvain ♀

18(13′). Underside of hindwing with crescent-shaped gray spot at base of Cu veins, spot faint from upperside (Figs. 291–292); western United States (Fig. 541) ..... *S. praefica* (Grote) ♂ ♀

18′. Underside of hindwing lacking crescent-shaped gray spot at base of Cu veins 19

19(18). Forewing with a rufous area between antemedial and postmedial lines ventral to Cu and CuA2 veins that extends to outer margin; hindwing veins with light brown scales from junction of Rs and M1 to margin (Figs. 296–299) ..... *S. ornithogalli* (Guenée) ♂ ♀

19′. Forewing lacking a rufous area between antemedial and postmedial lines ventral to Cu and CuA2 veins that extends to outer margin; hindwing veins with white scales at junction of Rs and M1(Figs. 293–295, 300) 20

20(19). Forewing with a variably shaped elliptical circle of black scales below vein Cu between the antemedial and postmedial lines; hindwing with apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales (Fig. 300); Florida throughout the Caribbean (Fig. 543) ..... *S. pulchella* (Herrich-Schäffer) ♂ ♀

20′. Forewing lacking an elliptical circle of black scales below vein Cu between the antemedial and postmedial lines; hindwing immaculate except for a small patch of gray scales at apex (Figs. 293–295); Venezuela and Colombia to northern Argentina and southern Brazil (Fig. 542) ..... *S. marima* (Schaus) ♂ ♀

Adult Descriptions

Spodoptera exigua (Hübner)

Figs. 18, 25, 38, 47, 59, 68, 77, 85, 95, 105, 116, 124, 151–152, 172–180, 308, 338, 370, 402, 434, 471–473, 522

Noctua exigua Hübner 1808: plate 78, figure 362.
Noctua fulgens Geyer 1832: plate 168, figure 796.
Caradrina pygmaea Rambur 1834: 384, plate 8, figure 2; Walker 1856: 188.
Caradrina junceti Zeller 1847: 447.
Laphygma caradrinoides Walker 1856: 190.
Caradrina flavimaculata Harvey 1876: 54.
Caradrina sebghana Austaut 1880: 212.
Caradrina venosa Butler 1880a: 7.
Prodenia caradrinoides; Cotes & Swinhoe 1888: 326.
Laphygma flavimaculata; Smith 1893: 168; Grote 1895: 42; Hampson 1909: 264.
Laphygma exigua; Walker 1856: 188; Cotes & Swinhoe 1888: 327; Swinhoe 1890: 227. Hampson 1909: 265; Warren *in* Seitz 1914a: 322; Barnes & McDunnough 1917: 67; Draudt 1926: 256; McDunnough 1938: 96.
Laphygma exigua subsp. *antipodea* Warren *in* Seitz, 1914a: 323.
Spodoptera exigua; Boursin 1964: 238; Forster & Wohlfahrt 1971: 159; Brown & Dewhurst 1975: 245; Franclemont & Todd 1983: 141; Todd & Poole 1980: 726; Goater 1983: 275; Poole 1989: 923; Edwards 1996: 324; Poole & Gentili 1996: 774; Kononenko *et al.* 1998: 233.
Douzdrina protector de Laever 1985: 149; [synonymized by Yela 1985]: 212.

Diagnosis.—This is a small moth with forewing ground color light brown to pale gray, a round, cream, orbicular spot centered with pale rufous, and hindwing with veins covered with light brown scales to base (Figs. 172–180). *Spodoptera exigua* has a cosmopolitan distribution. In the New World the female of *S. frugiperda* is most similar, but *S. exigua* can be distinguished by the lack of brown scales on veins at base of hindwing. In the male genitalia the cucullus has a round apex and sacculus is not well differentiated from valve (Figs. 308, 338). In *S. frugiperda* the cucullus has a truncate apex and sacculus is well differentiated (Figs. 323, 353). In *S. exigua* the female genitalia has an elongate corpus bursa (Fig. 402), compared to *S. frugiperda* with a round corpus bursa (Fig. 417). In the Old World *S. exigua* can be confused with the female of *S. cilium*, which has a similar orbicular spot that can be completely cream or centered with buff to brown (Figs. 182, 184–185, 187–188), and *S. pecten* (Figs. 196, 198, 200, 202–203). The color of the hindwing veins can be used to separate *S. exigua* from either *S. cilium* or *S. pecten* which have white veins near the base. Female genitalia are most similar to *S. pecten* (Fig.

405), but the ductus bursae is much shorter in *S. exigua*.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream, scales mixed with brown and black medially; median segment mixed with black and brown scales in basal half, cream apically; apical segment a mixture of cream, brown, and black scales. Frons with short scales cream; long scales cream to rufous; lateral spots at eye margin black; vertex cream (variably mixed with brown and black). Antenna filiform; scape cream and brown; flagellum cream (annulated brown becoming wholly brown at mid-length).

Thorax: Patagium light brown mixed with white scales, brown along apical margin. Tegula brown. Mesothorax a mixture of brown and light brown scales. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous (sometimes rufous scales present), subapical spot absent; tarsal segments fuscous with cream apical rings. Mesothoracic femur fuscous and cream; tibia fuscous and cream, inner spur more than twice length of outer spur, mediolateral surface sparsely scaled on both spurs; tarsal segments fuscous with cream apical rings. Metathoracic femur fuscous and cream; tibia fuscous and cream; first tarsal segment cream, remainder as in other legs.

Forewing: Length, 11–14 mm; ground color light brown to cream; basal line absent; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line black; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot round, cream, with pale rufous center; reniform spot with cream border, center variable with a combination of rufous, light brown, and or black scales; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line black, indistinct, from just below costa to posterior margin, wavy; postmedian band undifferentiated; black scale patches in middle of cells in postmedian area absent; subterminal line absent; apex lacking a white patch; black triangular-shaped spots along outer margin; fringe pale gray. Underside ground color a mixture of light brown and white scales, a slightly darker area covering discal cell; outer margin with black spots; reniform spot absent.

Hindwing: Ground color white; apex, outer margin, and veins with light brown scales; fringe white. Underside ground color white; costal cells C and Sc cream speckled with pale gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum cream; venter cream; distolateral black spots on sternites; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus curved in basal half; slender, gradually narrowing toward pointed apex; setae few or absent. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa bent in basal fifth (Figs. 308, 338). Costal process absent. Cucullus apex rounded; produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, narrow, slightly curved, apex round; extends to just below apex of valve (Figs. 308, 338). Clasper proper absent. Clavus absent. Sacculus narrow, width less than 0.2 length, tapering distally; apex pointed. Valvula wider than valve; not differentiated from valve; indentation absent. Coremata moderately elongate, approximately 0.5 or less length of valve; no distinct lobes. Juxta a narrow elliptical band, median process narrow with grooved apex, ventral margin convex. Anellus with minute granules. Vinculum a broad U-shape with bowed arms and a robust base. Aedoeagus straight; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; short, extending to just beyond apex of aedoeagus; cornuti in form of minute flat granules; lateral cornutal patch absent; dense cornutal patch subapical on vesica; distal cornutus a large spine.

Adult Female.—Essentially as described for male except:

Forewing: Length, 12.5–14 mm.

Abdomen: Fine dense scales on 8th segment whitish.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae membranous. Corpus bursae elongate,

length greater than twice width; smooth. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; forming less than a 30 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 99.

Type material.—*Noctua exigua* Hübner. The specimen illustrated in Hübner (1808, plate 78, figure 362) is a fair representation of *S. exigua* and the specimen the illustration depicts is considered the holotype. Type locality: Unknown.

Noctua fulgens Geyer. The type is apparently lost. Type locality: [Italy]: [Sicily].

Caradrina pygmaea Rambur. The type is apparently lost. Type locality: Marseille, France.

Caradrina junceti Zeller. The lectotype ♂ [BMNH, **here designated**] is labeled: Zell. Coll.,1884; Spain, Caralonia, 3-VII; *junceti*, var. b., Cat. 3 Ful; Noctuidae genitalia slide No. 3890 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 179. Type locality: Caralonia, Spain. The following syntypes become paralectotypes: (1) ♀, Label data: Zell. Coll.,1884; Spain, Caralonia, 3-VII; *junceti* ♀, Cat. 3 Ful; Noctuidae genitalia slide No. 3936 ♀. (2) ♀, Label data: Zell. Coll.,1884; Spain, Caralonia, 3-VII; *junceti* ♀, Cat. 3 Ful. (3) ♂, Label data: Zell. Coll.,1884; *junceti* ♂, Cat. 3 Ful; Noctuidae genitalia slide No. 589 ♂.

Laphygma caradrinoides Walker. The holotype ♂ [BMNH] is labeled: C. Colony [South Africa], 40-6-26; *Laphygma_ caradrinoides;* Noctuidae genitalia slide No. 594 ♂. Type locality: C. Colony [South Africa].

Caradrina flavimaculata Harvey. The lectotype ♂ (BMNH, **here designated**] is labeled: syntype 3481, Californ. [United States]; California, Grote Coll., *Caradrina flavimaculata* Harvey; Noctuidae genitalia slide No. 1598 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 178. Type locality: California, United States of America.

Caradrina sebghana Austaut. The type is apparently lost. Type locality: Algeria.

Caradrina venosa Butler. The holotype ♀ [BMNH] is labeled: Hawaii, Honolulu, T. Blackburn, 80-31; *Caradrina venosa* Butler type; Noctuidae genitalia slide No. 1658 ♀. Type locality: Honolulu, Hawaii, United States of America.

Laphygma exigua subsp. *antipodea* Warren. The lectotype ♂ [BMNH, **here designated**] is labeled: N. S. Wales [Australia], 1904.12.; Broken Hill; Noctuidae genitalia slide No. 595 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 176. The following syntypes become paralectotypes: (1) ♂, Label data: Broken Hill; N. S. Wales [Australia], 1904.12., ♂. (2) ♂, Broken Hill; N. S. Wales [Australia], 1904.12., ♂.

Material Examined.—Specimens were seen from the following countries: Aldabra Atoll, Bermuda, Canary Islands [Spain], Costa Rica, Dominica, Dominican Republic, Egypt, El Salvador, French Guiana, Germany, Guatemala, Honduras, India, Iran, Lebanon, Madagascar, Mexico, Pakistan, Panama, Papua New Guinea, Philippines, South Africa, Sri Lanka, Syria, Taiwan, Thailand, United States, Venezuela, Zimbabwe.

Distribution (Fig. 522).—*S. exigua* is the only cosmopolitan species in the genus. It has been found on all continents except Antarctica. It can migrate long distances and has been found in Sweden, Finland, and Latvia (Mikkola & Salmensuu 1965). Northern temperate regions are typically out of the breeding range of *S. exigua*. In the New World this species can reach southern Canada and is found throughout the United States. It occurs throughout Mexico and as far south as French Guiana and Venezuela (Todd & Poole 1980).

Discussion.—The forewing ground color in *S. exigua* can vary from light brown to pale gray. The pattern can also be distinct or faded. *Spodoptera exigua* is not sexually dimorphic. Morphological studies of the adult were detailed in Dong, *et al.* (1980).

There is a tremendous amount of economic literature on *S. exigua* because of its importance not only as a pest but as an experimental animal used in parasitoid rearings, host plant preference studies, testing bio-control agents, and physiological experiments.

Spodoptera cilium Guenée

Figs. 20, 41, 63, 86, 98, 113, 133, 138, 181–189, 309, 339, 371, 403, 435, 523

Spodoptera cilium Guenée *in* Boisduval & Guenée 1852a: 156; Walker 1856: 187; Cotes & Swinhoe 1888: 325; Swinhoe 1890: 227; Boursin 1964: 238; Brown & Dewhurst 1975: 251; Holloway 1989: 134; Poole 1989: 922.

Laphygma cycloides Guenée *in* Boisduval & Guenée 1852a: 157; Walker 1856: 190; Viette 1951: 160.
Spodoptera capicola Herrich-Schäffer [1854]: wrapper plate 27, fig. 131; Walker 1856: 191; Boursin 1961: 391.
Caradrina latebrosa Lederer 1855: 205.
Caradrina insignata Walker 1857a: 295; [synonymized by Poole 1989: 924].
Caradrina orbicularis Walker 1857a: 294; [synonymized by Poole 1989: 925].
Caradrina praeterita Walker 1857a: 294; [synonymized by Poole 1989: 925].
Laphygma procedens Walker 1857b: 721; [synonymized by Poole 1989: 925].
Laphygma obliterans Walker 1862b: 87; [synonymized by Poole 1989: 924].
Laphygma imperviata Walker 1865a: 651; [synonymized by Poole 1989: 924].
Laphygma retrahens Walker 1870: 126; [synonymized by Poole 1989: 925].

Diagnosis.—Sexually dimorphic, male lighter and with a more distinct wing pattern than in female. Male with antenna serrate (Fig. 20). Forewing ground color more gray than in *S. pecten*. Male genitalia with ampulla and clasper proper present (Figs. 309, 339); aedoeagus with a large dorsal spine at apex. Female genitalia with distal margin of ventral plate of ostium bursa a long central groove leading into ductus bursae (Fig. 435); fine dense scales on 8th segment whitish. Similar to *S. exigua*, especially females. *Spodoptera cilium* with hindwing veins white, veins infuscated with gray in *S. exigua*.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with a black dorsal patch; median segment black mixed with cream scales; apical segment black, apex cream. Frons with short scales cream; long scales cream to light brown; lateral spots at eye margin absent; vertex cream to pale rufous. Antenna serrate; scape cream to light brown; flagellum cream (annulated brown becoming wholly brown at mid-length).

Thorax: Patagium pale grayish brown with median band fuscous to grayish brown with a few fuscous scales representing median band. Tegula light brown and grayish brown. Mesothorax light brown to grayish brown. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur cream and fuscous; tibia cream and fuscous, inner spur more than twice length of outer spur, mediolateral surface thinly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; first tarsal segment cream mixed with fuscous, tarsal segments 2–5 fuscous with cream apical rings.

Forewing: Length, 9–13 mm; ground color light brown to brown; basal line black; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line black; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot round, cream, with buff to brown center, outlined in black (spot can be completely cream); reniform spot round, black; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line black, indistinct, from just below costa to posterior margin, wavy; postmedian band undifferentiated; black scale patches in middle of cells in postmedian area absent; subterminal line white, indistinct; apex lacking a white patch; black triangular-shaped spots along outer margin; fringe gray. Underside ground color pale gray; outer margin with black spots; reniform spot darker, indistinct to absent.

Hindwing: Ground color white; gray scales along apex and outer margin; fringe white (female with fringe light brown to pale gray at apex and median line becoming white toward anal veins). Underside ground color white; costal cells C and Sc cream speckled with pale gray scales; outer margin spots absent (female with pale gray spots in middle of cells, becoming indistinct toward anal cell).

Abdomen: Dorsum gray; venter cream and gray; disto-lateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus curved in basal half; slender, gradually narrowing toward pointed apex; setae numerous, elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa sinuate (Figs. 309, 339). Costal process an

indistinct swelling bearing setae located in middle of costa; perpendicular to costa of valve. Cucullus apex round; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a pointed apex; extending to moderately below apex of valve (Figs. 309, 339). Clasper proper triangulate with pointed apex. Clavus absent. Sacculus broadest at base, gradually tapering distally; apex truncate. Valvula narrower than valve; slightly differentiated from valve, apex not separate; apex pointed; indentation absent. Coremata reduced, closely appressed to sacculus; no distinct lobes. Juxta a rectangular band, median process elongate, expanding into an apical plate, ventral margin straight to convex. Anellus membranous. Vinculum round. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving dorsally; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon; composed of granular spines with a very large basal spine; dense cornutal patch on apical diverticulum; distal cornutus absent.

Adult Female.—Essentially as described for male except:

Forewing: Length, 11–15 mm.

Abdomen: Fine dense scales on 8th segment whitish.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin a long central groove leading into ductus bursae; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae membranous. Corpus bursae bulbous, length less than twice width; a few striae. Signum in apical half of corpus bursae; moderately elongate, length between 0.66–1.1 mm; forming less than a 30 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 104.

Type material.—*Spodoptera cilium* Guenée. Syntypes: The type material was not located during this study and is considered lost. The neotype ♂ [USNM, **here designated**] is labeled: SOUTH AFRICA: Cape Prov.; Ravens Wood, 125 meters; Keiskama River, nr. Rt. N2; bridge, 5 March 1978; D. & M. Davis, B. Akerbergs. USNM ENT 00061924. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 181. Type locality: Cape Province, South Africa.

Laphygma cycloides Guenée. The lectotype ♀ is deposited in MNHP and was designated by Viette (1951). Type locality: Cape of Good Hope, South Africa.

Spodoptera capicola Herrich-Schäffer. The type is apparently lost. Type locality: Cape Province, South Africa.

Caradrina latebrosa Lederer. The type is in Museum für Naturkunde, Humboldt University, Berlin. Type locality: Cyprus.

Caradrina insignata Walker. The holotype ♂ [BMNH] is labeled: S. Africa: A. Smith: 44-6; 29. *Caradrina insignata*; Noc. Gen. Slide No. 3803 ♂. Type locality: South Africa.

Caradrina orbicularis Walker. The lectotype ♂ [BMNH, **here designated**] is labeled: S. Africa, A. Smith, 44-6; 26. *Caradrina orbicularis;* Noc. Gen. Slide No. 3805 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of pest species and is illustrated in Fig. 187. Type locality: South Africa.

Caradrina praeterita Walker. The lectotype ♀ [BMNH, **here designated**] is labeled: S. Africa, A. Smith, 44-6; 27. *Caradrina praeterita*; Noc. Gen. Slide No. 3804 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of pest species and is illustrated in Fig. 188. Type locality: South Africa.

Laphygma procedens Walker. The holotype ♂ [BMNH] is labeled: Holotype, S. Leone, D.F. Morgan, 38, 11-8, 528; *Laphygma procedens.* Type locality: Sierra Leone.

Laphygma obliterans Walker. The type(s) are in University Museum, Oxford University, Oxford. Type locality: Cape, South Africa.

Laphygma imperviata Walker. The type material is lost. Type locality: South Africa.

Laphygma retrahens Walker. The type material is lost. Type locality: Mount Sinai, Egypt, (ex Convent Gardens).

Material Examined.—Specimens were examined from the following countries: Algeria, Angola, Burma, China, Comoro Islands, Egypt, Ethiopia, Ghana, India, Indonesia, Iran, Ivory Coast, Kenya, Lebanon, Madagascar, Malawi, Malaysia, Mauritius, Morocco, Nigeria, Pakistan, Philip-

pines, Réunion, São Tomé, Senegal, Seychelles [France], Singapore, South Africa, Sri Lanka, Taiwan, Tanzania, Thailand, Tunisia, Uganda, Vietnam, Zimbabwe.

Distribution (Fig. 523).—This species has been recorded from the southern Palaearctic in southern France and Rhodes, Greece, eastward to Lebanon, Israel, Afghanistan, Iran, Iraq, Bahrain, the Arabian Peninsula, and China. It is widely distributed across Africa, Madagascar, Comoro Islands, Seychelles, Mauritius, and Réunion. In the Oriental Region it has been recorded from Burma, India, Sri Lanka, Thailand, Sumatra, Java, Malaysia, Singapore, and the Philippines. In Australasia it occurs in Borneo, Sulawesi, Santa Cruz in the Solomon Islands, and Papua New Guinea (Brown & Dewhurst 1975).

Discussion.—Variation occurs in the forewing color ranging from light brown to brown. Sexual dimorphism is less evident than in the preceding species. The male tends to have more pattern in the forewing.

Hampson (1909) and Warren (1914a) treated *S. cilium* as a synonym of *Spodoptera abyssinia* Guenée, which is referable to the species *Ariathisa abyssinia* (Guenée) (Poole 1989).

Spodoptera depravata (Butler)

Figs. 123, 190–193, 310, 340, 372, 404, 436, 524

Agrotis depravata Butler 1879: 360.
Luperina inutilis Alpheraky 1897: 171, plate 2 fig. 10.
Rusidrina rasdolnia Staudinger 1892: 491, plate 7, fig. 9.
Euxoa kaolina Bryk 1949: 57.
Spodoptera depravata; Sugi 1982: 764; Poole 1989: 922; Kononenko *et al.* 1998: 234.

Diagnosis.—Most similar to *S. cilium,* but male of *S. depravata* with bipectinate antenna (Fig. 19). Forewing ground color light brown, pattern in male less distinct than in *S. cilium.* Male genitalia with ampulla narrower and apex more produced than in *S. umbraculata* (compare Figs. 310, 340 to 312, 342). Female genitalia with distal margin of ventral plate of ostium bursa straight (Figs. 404, 436); signum shorter and at a steeper angle than in *S. umbraculata* (compare Fig. 404 to 406).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream variably mixed with gray scales; median segment cream variably mixed with gray scales; apical segment cream. Frons with short scales cream; long scales cream; lateral spots at eye margin absent; vertex cream. Antenna bipectinate; scape cream; flagellum cream.

Thorax: Patagium light brown with a brown median transverse band. Tegula light brown. Mesothorax cream to light brown. Underside of thorax cream. Prothoracic femur cream to fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur cream; tibia cream, inner spur more than twice length of outer spur, mediolateral surface thinly devoid of scales on both spurs; tarsal segments cream with pale fuscous bases. Metathoracic femur cream; tibia cream (can have fuscous scales present); tarsal segments cream.

Forewing: Length, 12–14 mm; ground color light brown; basal line absent; longitudinal black dash at base absent; R vein not contrasting in color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line absent; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, indistinct, cream, outlined in brown; reniform spot round, black; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line (can be indistinct to absent); postmedial line black, from just below costa to posterior margin, wavy; postmedian band undifferentiated; black scale patches in middle of cells in postmedian area absent; subterminal line white, indistinct (can be absent on worn specimens); apex lacking a white patch; minute black spots along outer margin to black triangular-shaped spots along outer margin; fringe pale gray. Underside ground color pale gray; outer margin with black spots becoming absent with only the margin gray; reniform spot darker, indistinct.

Hindwing: Ground color white suffused with pale gray; apex, outer margin, and veins with pale gray scales; fringe pale gray. Underside

ground color pale gray, especially along costa, outer margin, and veins, proximal half of wing cells white; outer margin spots absent; no spot on underside.

Abdomen: Dorsum pale gray; venter pale gray; disto-lateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus curved in basal half; maintaining width throughout three-fourths length, narrowing to pointed apex; setae few or absent. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa sinuate (Figs. 310, 340). Costal process a minute knob; in middle of costa; perpendicular to costa of valve. Cucullus apex round; produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a pointed apex; extending to just below apex of valve (Figs. 310, 340). Clasper proper absent. Clavus absent. Sacculus broadest at base, gradually tapering distally; apex pointed. Valvula narrower than valve; well differentiated from valve, apex free; apex round; indentation absent. Coremata reduced, closely appressed to sacculus; no distinct lobes. Juxta a rectangular band, median process elongate, expanding into an apical plate, ventral margin straight to convex. Anellus membranous. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curved dorsally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; length moderate, to less than middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon; large spines; dense cornutal patch on apical diverticulum; distal cornutus absent.

Adult Female.—Essentially as described for male except:

Forewing: Length, 16 mm.

Thorax: Prothoracic femur cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical ring on segments 3 and 4. Mesothoracic femur cream; tibia cream, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments cream with pale fuscous bases. Metathoracic femur cream; tibia cream (can have fuscous scales present); tarsal segments cream.

Abdomen: Fine dense scales on 8th segment whitish.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae moderately elongate (length 2–3 times width); completely sclerotized. Appendix bursae membranous. Corpus bursae bulbous, length less than twice width; a few striae. Signum in apical half of corpus bursae; short, length less than 0.65 mm; forming less than a 30 degree angle with vertical axis of corpus bursae.

Larva.—Unknown.

Type material.— *Agrotis depravata* Butler. The lectotype ♂ [BMNH, **here designated**] is labeled: Japan, Yokohama, H. Pryer, 79-48. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 191. Type locality: Yokohama, Japan.

Luperina inutilis Alpheraky. The syntypes, 7 ♂, 1 ♀, are deposited in the Zoological Institute, Academy of Sciences, Leningrad. Type locality: Korea.

Rusidrina rasdolnia Staudinger. The holotype ♂ is deposited in the Museum für Naturkunde der Humboldt University, Berlin. Type locality: Amur district, Rasdolnaja, [SE Siberia], [Russia].

Euxoa kaolina Bryk. The holotype ♂ is deposited in the Naturhistoriska Riksmuseet, Stockholm. Type locality: Shuotsu, Korea.

Material Examined.—Specimens were examined from the following countries: China, Japan, Korea.

Distribution (Fig. 524).—In eastern Palaearctic from SE Siberia (Russia) to Korea and Japan, south to Szechuan, China.

Discussion.—The forewing ground color can vary from light brown to brown and the pattern can be quite distinct or faded. Sexual dimorphism is present in the antennal form with the male having bipectinate antennae.

***Spodoptera pecten* Guenée**

Figs. 104, 194–203, 311, 341, 373, 405, 437, 525

Spodoptera pecten Guenée, *in* Boisduval & Guenée 1852a: 155; Walker 1856: 186; Hampson 1909: 252; Warren *in* Seitz 1914b: 320; Holloway 1976: 12; Holloway 1989: 134; Poole 1989: 925; Kononenko *et al.* 1998: 234.

Agrotis infixa Walker 1862a: 186. **New synonym.**
Spodoptera infixa; Poole 1989: 924.
Spodoptera insulsa Walker 1865a: 648; Poole 1989: 924. **New synonym.**
Spodoptera erica Butler 1880b: 675.
Spaelotis uniformis Swinhoe 1890: 226.
Caradrina pectinata Hampson 1894: 264.
Elydna speciosa Rothschild 1920: 117 [synonymized by Poole 1989: 925].

Diagnosis.—Sexually dimorphic, male darker than female and with a more distinct wing pattern than in female. Male with antenna bipectinate (Fig. 19). Forewing ground color browner than in *S. cilium.* Male genitalia with ampulla moderately broad, curved distally with a pointed apex (Figs. 311, 341). Female genitalia with distal margin of ventral plate of ostium bursa straight (Figs. 405, 437).

Description. Adult Male.—*Head:* Basal segment of labial palpus black with longer ventral scales cream; median segment black, variably mixed with brown and cream, apex cream (lightly speckled with brown); apical segment black, apex cream. Frons with short scales cream to brown; long scales cream to light brown; lateral spots at eye margin absent; vertex cream to pale rufous. Antenna bipectinate; scape cream to light brown; flagellum cream annulated brown, becoming completely cream toward apex.

Thorax: Patagium cream to brown, or grayish brown mixed with fuscous and fuscous median band. Mesothorax cream to light brown, or gray mixed with fuscous scales. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot black; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur cream and rufous; tibia cream and rufous, inner spur more than twice length of outer spur, mediolateral surface thinly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments cream, segments 2–5 pale fuscous at base.

Forewing: Length, 12–14 mm; ground color light brown to brown; basal line black (indistinct); R vein not contrasting in color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line black; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, indistinct, cream, outlined in brown (can be absent); reniform spot round, black; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line brown, indistinct, outlined in white in posterior third; postmedian band undifferentiated (a few specimens can have an indistinct round spot along subterminal line); black scale patches in middle of cells M2 to CuA1, indistinct, with or without faint patches in M1 in postmedian area; subterminal line white, indistinct; apex lacking a white patch; black trapezoidal-shaped spots along outer margin; fringe gray. Underside ground color light brown to brown; outer margin with black spots; reniform spot darker, indistinct.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales; fringe light brown to pale gray at apex and median line, becoming white toward anal veins. Underside ground color white; costal cells C and Sc cream, speckled with pale gray scales; outer margin with a few faint gray spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum cream to pale gray; venter cream; disto-lateral black spots on sternites (indistinct); 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus curved in basal half; maintaining width throughout three-fourths length, narrowing to pointed apex; setae numerous. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa bent in basal fifth (Figs. 311, 341). Costal process a minute knob; in middle of costa; perpendicular to costa of valve. Cucullus apex round; produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a pointed produced apex; extending moderately below apex of valve (Figs. 311, 341). Clasper proper absent. Clavus absent. Sacculus broadest at base, gradually tapering distally; apex truncate. Valvula narrower than valve; slightly differentiated from valve, apex not separate; apex pointed; indentation pronounced, ventral margin well sclerotized. Coremata re-

duced, closely appressed to sacculus; no distinct lobes. Juxta a rectangular band, median process elongate, expanding into an apical plate, ventral margin straight to convex. Anellus membranous. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; length moderate, not quite extending to middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon; large spines; dense cornutal patch on apical diverticulum; distal cornutus absent.

Adult Female.—Essentially as described for male except:

Thorax: Prothoracic femur cream and fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, light brown and rufous, subapical spot fuscous; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur cream; tibia cream; inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments cream. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments cream, segments 2–5 pale fuscous at base.

Forewing: Length, 11–14 mm. Basal line absent; antemedial line absent; black scale patches in middle of cells in postmedian area absent; minute black spots along outer margin; fringe light brown.

Abdomen: Disto-lateral black spots on sternites absent. Fine dense scales on 8th segment whitish.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae elongate (length greater than 3 times width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; a few striae. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; forming less than a 30 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 104.

Type material.—*Spodoptera pecten* Guenée. The holotype ♂ [BMNH] is labeled: Java ♂ E.I.C.; Noctuidae genitalia slide No. 3810 ♂. Type locality: Java, Indonesia.

Agrotis infixa Walker. The type(s) are deposited in the University Museum, Oxford University. Type locality: Borneo, Sarawak, Indonesia.

Spodoptera insulsa Walker. The holotype ♀ [BMNH] is labeled: [No locality label on specimen]; Holotype; *Spodoptera insulsa* 1954/432; Noctuidae genitalia slide No. 3813 ♀. Type locality: Java, Indonesia.

Spodoptera erica Butler. The lectotype ♀ [BMNH, **here designated**] is labeled: Formosa, Talkow, H. E. Hobson, 80-115; Noctuidae genitalia slide 3812 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 198. Type locality: Taiwan. The following syntypes become paralectotypes: (1), ♀, Label data: Formosa [Taiwan], Talkow, H. E. Hobson, 80-115. (2), ♂, Label data: Formosa [Taiwan], Talkow, H. E. Hobson, 80-115.

Spaelotis uniformis Swinhoe. The lectotype ♀ [BMNH] is labeled: Burma, Bhamo, X. 82, 91-55; Noctuidae genitalia slide No. 3472 ♀. Type locality: Bhamo, Burma. Swinhoe (1890: 226) described *uniformis* from one specimen of unknown sex, from Bhamo, Burma. Hampson (1909: 253 listed "1 ♂ type *uniformis*" from his list of specimens from Burma. This can be inferred as a lectotype designation and this specimen is the one mentioned above and is illustrated in Fig. 203.

Caradrina pectinata Hampson. The holotype ♂ [BMNH] is labeled: Naga Hills, 1500 ft., Sept.-Oct. 1889, W. Doherty; *Caradrina, pectinata,* Hmpson. holotype ♂; 1954/479; Noctuidae genitalia slide No. 3471 ♂. Type locality: Naga hills, India.

Elydna speciosa Rothschild. The lectotype ♀ [BMNH, **here designated**] is labeled: Pasir Ganting, W. Sum. lat. 2° S, June 1914, (Robinson & Kloss); Rothschild, Bequest, B.M. 1939-1; *Elydna, speciosa,* Rothsch. Type; Rothschild, Bequest, B.M. 1939-1; Noctuidae genitalia slide No. 3873 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 202. The following syntype becomes a paralectotype: ♀, Label data: Pasir Ganting, W. Sum.[atra] lat. 2° S, June 1914, (Robinson & Kloss); Rothschild, Bequest, B.M. 1939-1.

Material examined.—Specimens were examined from the following countries: Burma, China, India, Indonesia, Japan, Malaysia, Nepal, Papua

New Guinea, Philippines, Singapore, Sri Lanka, Taiwan, Thailand, Vietnam.

Distribution (Fig. 525).—This species is distributed in eastern and southeastern Asia from Nepal to Sri Lanka and east to Vietnam, Malaysia, China, Japan, and Taiwan. In the Indo-Pacific area it is found in Indonesia and the Philippines.

Discussion.—Some variation exists in the ground color of the forewing ranging from light brown to brown. *Spodoptera pecten* is sexually dimorphic. The male has bipectinate antenna and a more darkly shaded forewing than does the female. The orbicular and reniform spots are less distinct in the female.

In Poole (1989) the species *infixa* and *insulsa* were listed as synonyms of *S. cilium*. These are actually synonyms of *S. pecten*.

Spodoptera umbraculata (Walker)

Figs. 32, 204–206, 312, 342, 374, 406, 438, 526

Eumichtis? umbraculata Walker 1858: 1717.
Agrotis enunciatus Lucas 1892: 85.
Hadena andrias Meyrick 1902: 27.
Spodoptera umbraculata; Hampson 1909: 252; Warren *in* Seitz 1914b: 320; Poole 1989: 925; Edwards 1996: 324.

Diagnosis.—Color and pattern similar to *S. mauritia* and *S. triturata*, but the overall pattern of *S. umbraculata* is more distinct with an obvious white orbicular spot and associated white bar in the male (Figs. 204–205). Male with antenna bipectinate (Fig. 19). Male genitalia with ampulla wider and apex less produced than in *S. depravata* (compare Figs. 310, 340 with 312, 342). Female genitalia with distal margin of ventral plate of ostium bursa sinuate (Fig. 406, 438); signum longer and almost parallel to ventral plate of ostium bursa (Fig. 406).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment rufous with black transverse bar at 2/3 length; apical segment rufous, apex cream (can be sprinkled with black scales). Frons with short scales cream; long scales black and rufous (scattered with cream scales); lateral spots at eye margin absent; vertex black and cream (sometimes mixed with rufous scales). Antenna bipectinate; scape cream to rufous; flagellum cream, annulated black in basal fifth.

Thorax: Patagium banded, basal band rufous mixed with black, a thin black row of scales separating white median band, distal band light brown. Tegula light brown and black. Mesothorax light brown to brown with variable mix of white and fuscous scales. Underside of thorax white. Prothoracic femur light brown; tibia with lateral scale tufts not extending beyond first tarsal segment, rufous and cream, subapical spot black; tarsal segments fuscous with cream apical rings. Mesothoracic femur light brown and cream; tibia rufous and cream, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments fuscous with cream apical rings.

Forewing: Length, 14–16 mm; ground color gray; basal line black; longitudinal black dash at base absent; R vein not contrasting in color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line brown, indistinct; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, cream, bordered by white distally between R and Cu veins; reniform spot round, black; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line black, from just below costa to posterior margin, wavy; postmedian band undifferentiated; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area (patches in cells R4 and R5 can be missing in worn specimens); subterminal line white, curved; apex lacking a white patch; black triangular-shaped spots along outer margin; fringe gray and rufous. Underside ground color pale gray; outer margin with black spots; reniform spot gray.

Hindwing: Ground color white; gray scales along apex and outer margin; fringe white. Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray and cream; venter rufous and cream; disto-lateral black spots on sternites; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus curved in basal half; slender, gradually narrowing toward pointed apex; setae numerous. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa sinuate (Figs. 312, 342). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex round; produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a pointed produced apex; extending to moderately below apex of valve (Figs. 312, 342). Clasper proper absent. Clavus absent. Sacculus broadest at base, gradually tapering distally; apex pointed. Valvula narrower than valve; well differentiated from valve, apex free; apex pointed; indentation pronounced, ventral margin well sclerotized. Coremata reduced, closely appressed to sacculus; no distinct lobes. Juxta a rectangular band, median process elongate, expanding into an apical plate, ventral margin straight to convex. Anellus membranous. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon; composed of large spines; dense cornutal patch on apical diverticulum; distal cornutus absent.

Adult Female.—Essentially as described for male except:

Head: Basal segment of labial palpus cream with a black dorsal patch; median segment cream with dark gray basal patch extending to middle; apical segment dark gray, apex cream. Frons long scales black and cream. Antennal scape cream and rufous (sometimes mixed with black scales).

Thorax: Prothoracic femur fuscous and cream; tibia cream, black, and rufous, subapical spot absent. Mesothoracic femur fuscous and cream; tibia fuscous and cream. Metathoracic femur fuscous and cream; tibia fuscous and cream.

Forewing: Length, 16–17.5 mm. Orbicular spot oval, cream, faintly outlined in black; reniform spot black outlined in white; white scales along Cu vein and bases of M3 and CuA1 veins absent; black scale patches short in middle of cells R4 to CuA1 in postmedian area (faint); fringe gray and white.

Hindwing: Fringe white with gray median line to anal vein.

Abdomen: Venter cream and pale gray; disto-lateral black spots on sternites (smaller than in male). Fine dense scales on 8th segment whitish.

Genitalia: Ventral plate of ostium bursa wider than high; distal margin sinuate; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae completely sclerotized. Corpus bursae bulbous, length less than twice width; a few striae. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; forming less than a 30 degree angle with vertical axis of corpus bursae.

Larva.—Unknown.

Type material.—*Eumichtis? umbraculata* Walker. The holotype ♂ [BMNH] is labeled: Queensland, Moreton B., Diggles, 57-180; *Eumichtis umbraculata;* Noctuidae genitalia slide No. 3473 ♂. Type locality: Moreton Bay, Queensland, Australia.

Agrotis enunciatus Lucas. The type(s) are deposited in the South Australian Museum, Adelaide. Type locality: Brisbane, Queensland, Australia.

Hadena andrias Meyrick. The holotype ♂ [BMNH] is labeled: Brisbane, Queensland; *Hadena, andrias,* Meyr; Noctuidae genitalia slide No. 3881 ♂. Type locality: Brisbane, Queensland, Australia.

Material Examined.—Specimens were examined from the following country: Australia.

Distribution (Fig. 526).—This species has a limited distribution in New South Wales and Queensland, Australia.

Discussion.—There is some variation in the amount of gray along the outer margin of the hindwing. Sexual dimorphism is present. The male has bipectinate antennae and a horizontal white band that extends from the orbicular spot and to the postmedial line. The female tends to have less dark shading in the forewing, especially the area between the antemedial and postmedial lines below the orbicular and reniform spots.

***Spodoptera pectinicornis* (Hampson)**

Figs. 167, 207–211, 313, 343, 375, 407, 439, 474–476, 526

Xanthoptera pectinicornis Hampson 1895: 300; 1896: 515.
Caradrina hennia Swinhoe 1901: 495; Holloway 1989: 135.
Athetis hennia; Poole 1989: 133.
Namangana pectinicornis; Hampson 1909: 545; Poole 1989: 677.
Spodoptera pectinicornis; Holloway 1989: 135.

Diagnosis.—Sexually dimorphic, male with forewing darker than female. Male antenna bipectinate (Fig. 19). Forewing pattern obscure, smaller than both *S. apertura* and *S. malagasy.* Male genitalia with valve much narrower (Figs. 313, 343) than in either *S. pecten* (Figs. 311, 341) or *S. cilium* (Figs. 309, 339). Ampulla long and narrow with a pointed apex (Figs. 313, 343). Female genitalia with signum small and round (Figs. 407, 439).

Description. Adult Male.—*Head:* Basal segment of labial palpus dark brown mixed with cream scales; median segment dark brown mixed with cream scales; apical segment dark brown, apex cream. Frons with short scales brown; long scales brown; lateral spots at eye margin absent; vertex brown mixed with light brown. Antenna bipectinate; scape brown mixed with cream; flagellum cream annulated brown, becoming completely cream toward apex.

Thorax: Patagium light brown with a median brown transverse band. Tegula brown. Mesothorax light brown. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, fuscous and cream subapical spot absent; tarsal segments fuscous with cream apical rings on segments 1 and 2. Mesothoracic femur cream and fuscous; tibia fuscous with cream median and apical bands, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments fuscous with cream apical rings. Metathoracic femur more cream than fuscous; tibia more fuscous than cream; tarsal segments more fuscous than cream with cream apical rings.

Forewing: Length, 8–8.3 mm; ground color brown; basal line absent; longitudinal black dash at base absent; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line absent; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot indistinct, rufous; reniform spot indistinct, rufous; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line a series of faint black spots; postmedian band undifferentiated; subterminal line absent; apex lacking a white patch; spots along outer margin absent; fringe brown. Underside ground color light brown; outer margin with black spots; reniform spot absent.

Hindwing: Ground color white suffused with light brown; costal area to vein Rs light brown, outer margin with light brown scales, vein M1 light brown; fringe white. Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin suffused with gray scales and with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Eighth tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; maintaining width throughout three-fourths length, narrowing to pointed apex; setae numerous. Scaphium elongate, well sclerotized. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 313, 343). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Valve narrowly rounded. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a pointed, produced apex; curved toward sacculus; extends beyond apex of valve (Figs. 313, 343). Clasper proper absent. Clavus a minute round projection. Sacculus broadest at base, gradually tapering distally; apex pointed. Valvula narrower than valve; slightly differentiated from valve, apex not separate; apex pointed; indentation absent. Coremata reduced, closely appressed to sacculus; no distinct lobes. Juxta a narrow rectangular band with ventrolateral-lateral projections, median process as wide as base, ventral margin straight with curved sides. Anellus membranous. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus.

Adult Female.—Essentially as described for male except:

Head: Basal segment of labial palpus cream; median segment cream; apical segment cream. Frons with short scales cream; long scales cream; vertex cream. Antenna scape cream; flagellum cream.

Thorax: Patagium cream. Tegula cream. Mesothorax cream. Prothoracic femur cream; tibia cream; tarsal segments cream. Mesothoracic femur cream; tibia cream; tarsal segments cream. Metathoracic femur cream; tibia cream; tarsal segments cream.

Forewing: Length, 8.3–9.3 mm. Ground color rufous; orbicular spot absent; reniform spot absent; postmedial line a broad brown band (can be faint); subterminal line reddish brown, indistinct; black triangular-shaped spots along outer margin. Underside ground color cream with light brown scales; outer margin with indistinct gray spots.

Hindwing: Ground color white; fringe white. Underside ground color white; costal cells C and Sc white speckled with light brown scales; outer margin spots absent.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae moderately elongate (length 2–3 times width); completely sclerotized. Appendix bursae membranous. Corpus bursae elongate, length greater than twice width; a few striae. Signum in apical half of corpus bursae; short, length less than 0.65 mm; almost vertical.

Larva.—See description, p. 104.

Type material.—*Xanthoptera pectinicornis* Hampson. The lectotype ♂ [BMNH] is labeled: Ceylon; 95-37; Hambantota: March. Type locality: Hambantota, Sri Lanka. In Hampson's original description of *pectinicornis* (1895: 300) there were 2 ♂ specimens, one from Calcutta, and the other from Hambantota, Ceylon. Hampson (1909: 545) listed "1 ♂ type" from Hambantota in his list of specimens from Ceylon. This can be inferred as a lectotype designation and this specimen is the one mentioned above and is illustrated in Fig. 207.

Caradrina hennia Swinhoe. The lectotype ♂ [BMNH, **here designated**] is labeled: [Borneo] Sarawak. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 211. The following syntypes become paralectotypes: (1) ♀, Label data: Sarawak; 5377; (2) ♂, Label data: Sarawak; (3) ♀, Label data: 1901-178 Sarawak; Borneo; Noctuidae ♀; Brit. Mus. Slide; No. 9980 ♀; (5) ♀, Label data: Sarawak; 1901: 178 ♀.

Material Examined.—Specimens were examined from the following countries: Bangladesh, Indonesia, Papua New Guinea, Singapore, Sri Lanka.

Distribution (Fig. 526).—This species is widely distributed in southern Asia and the Indo-Pacific Region including India, Sri Lanka, Bangladesh, Indonesia, and Papua New Guinea.

Discussion.—*Xanthoptera pectinicornis* was transferred to *Spodoptera* on the basis of its male and female genitalia (Holloway 1989).

Spodoptera apertura (Walker)

Figs. 64, 70, 78, 89, 112, 122, 212–216, 314, 344, 376, 408, 440, 527

Prodenia apertura Walker 1865a: 654; Cotes & Swinhoe 1888: 326.

Prodenia synstictis Hampson 1896: 511.

Prodenia leucophlebia Hampson 1902: 288; [synonymized by Brown & Dewhurst 1975: 253].

Laphygma leucophlebia; Hampson 1909: 259; Warren *in* Seitz 1914a: 322.

Laphygma connexa Wileman 1914: 166. **New synonym.**

Spodoptera connexa; Poole 1989: 922.

Spodoptera teferii Laporte *in* Rougeot 1984: 29; Poole 1989: 925. **New synonym.**

Laphygma apertura; Hampson 1909: 260; Warren *in* Seitz 1914a: 321.

Spodoptera apertura; Brown & Dewhurst 1975: 253; Holloway 1989: 135; Poole 1989: 922; Edwards 1996: 324; Kononenko *et al.* 1998: 235.

Diagnosis.—*Spodoptera apertura* is most similar in color and pattern to *S. malagasy.* Male antenna is less serrate in *S. apertura* than in *S. malagasy. Spodoptera apertura* has a white hindwing (Figs. 212–216), but it is light brown in *S. malagasy* (Figs. 217–218). Forewing is dark brown with middle portion of M vein and bases of CuA1 and CuA2 outlined in white. In the male genitalia, the uncus base is more slender and the sacculus apex is more pointed in *S. apertura* (Fig. 314) than in *S. malagasy* (Fig. 315). In the female genitalia, the ventral plate of ostium bursa and ductus bursae are more slender in *S. apertura* (Fig. 408) than in *S. malagasy* (Fig. 409).

Description. Adult Male.—*Head:* Basal segment of labial palpus dark brown; median segment mixed with black and brown scales in basal half, cream apically (suffused with rufous); apical

segment dark brown. Frons with short scales brown; long scales brown; lateral spots at eye margin absent; vertex brown. Antenna serrate; scape brown; flagellum cream and brown.

Thorax: Patagium brown with a black and light brown median band, light brown apical margin. Tegula brown. Mesothorax brown. Underside of thorax cream. Prothoracic femur fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent, first tarsal segment cream, tarsal segment 2 fuscous with cream apical ring, tarsal segments 3–4 fuscous, tarsal segment 5 fuscous with cream apical ring. Mesothoracic femur cream and fuscous; tibia fuscous and cream, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and fuscous; tibia cream and fuscous; tarsal segments fuscous with cream apical rings.

Forewing: Length, 11–14 mm; ground color dark brown; basal line black; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line black, indistinct; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique trapezoid, cream, with a brown center, bordered by thin black lines; reniform spot cream outlined in black, center light brown to brown; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 and down vein CuA2 to postmedial line; postmedial line black, indistinct, from just below costa to posterior margin, wavy; postmedian band gray to brown; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches in postmedian area; subterminal line a light brown band bordered by white; apex lacking a white patch; dark brown square spots along outer margin; fringe gray. Underside ground color pale gray; outer margin spots absent; reniform spot gray.

Hindwing: Ground color white; a small patch of gray scales at apex (can be indistinct); fringe white. Underside ground color white; costal cells C and Sc cream speckled with pale gray scales; outer margin with a few faint gray spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum cream; venter gray; distolateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 314, 344). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a pointed, produced apex; extending beyond apex of valve (Figs. 314, 344). Clasper proper absent. Clavus a minute round projection. Sacculus broadest at base, gradually tapering distally; apex pointed. Valvula narrower than valve; well differentiated from valve, apex free; apex pointed; indentation absent. Coremata reduced, closely appressed to sacculus; no distinct lobes. Juxta a narrow rectangular band with ventrolateral-lateral projections, median process as wide as base, ventral margin straight with curved sides. Anellus membranous. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch quadrate; short, extending to just beyond apex of aedoeagus; cornuti in form of minute flat granules; lateral cornutal patch absent; dense cornutal patch subapical on vesica; distal cornutus an ovate plate with large spines at apex.

Adult Female.—Essentially as described for male except:

Forewing: Length, 14.5 mm.

Abdomen: Fine dense scales on 8th segment whitish.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; a few striae. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; forming greater than a 45 degree angle to vertical axis of corpu bursae.

Larva.—Unknown.

Type material.—*Prodenia apertura* Walker. The following quote, which is in George Hampson's handwriting, is on the flyleaf of Volume 1–3 of Walker's catalogue in the Macrolepidoptera Sectional Library, Entomology Department, BMNH. It reads: "The species described by Walker in the Catalogue as being in Coll. Layard, from Ceylon were left, Mr. E.L. Layard states, by him with his brother in-law in Lincolnshire when he returned to the East & the collection has disappeared." (Kitching, pers. corr.) The neotype ♀ [ANIC, **here designated**] is labeled: 3 miles S. of; Port Macquarie,; NSW, 26 Mar 1965; I. F. B. Common; & M. S. Upton. SPOD 1656. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 212. Type locality: Sri Lanka.

Prodenia synstictis Hampson. The lectotype ♂ [BMNH] is labeled: Ceylon; Hambantota; J. Pole; 98-119. Type locality: Hambantota, Sri Lanka. Hampson (1896: 511) described *subterminalis* from 3 specimens of unknown sex, 2 specimens from Nilgris, and 1 specimen from Ceylon. Hampson (1909: 260) listed "1 ♂ type *synstictis*" from Hambantota, Ceylon. This can be inferred as a lectotype designation and this specimen is the one mentioned above and is illustrated in Fig. 215.

Prodenia leucophlebia Hampson. The ♂ lectotype [BMNH, **here designated**] is labeled: Karkloof, Natal, G.A.K. Marshall, 97-50; *Prodenia leucophlebia*, type ♂ Hmpsn.; Noctuidae genitalia slide No. 3836 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 214. Type locality: Karkloof, Natal, South Africa. The following syntype becomes a paralectotype: ♂, Label data: Natal, Karkloof, G.A.K. Marshall, 97-50.

Laphygma connexa Wileman. The lectotype ♂ [BMNH] is labeled: Kanshirei, Formosa, 1,000 ft., 10-XI-1908, A. E. Wileman. Type locality: Kanshirei, Taiwan. This specimen is illustrated in Fig. 213.

Spodoptera teferii Laporte. The holotype ♂ [MNHP] is labeled: 9env. Koffolé, 1800-2000 m Ethiopie, 8-XI-1973, P.C. Rougeot Leg.; Mission, P.-C. Rougeout, XI-XII 1973; TYPE; *Spodoptera teferii* Laporte, Holotype ♂, P.-C. Rougeout det. 19; 1314. Type locality: Koffolé, Ethiopia.

Material Examined.—Specimens were examined from the following countries: Australia, China, India, Madagascar, Sri Lanka, and Zaire.

Distribution (Fig. 527).—This species has an Ethiopian, Oriental, and Australasian distribution. In Africa it is known from Natal, Transvaal, Zimbabwe, Botswana, Cape Province, Zaire, Ethiopia, Tanzania, Madagascar, and the Comoro Islands. From the Oriental region it has been found in China, Taiwan, India, and Sri Lanka. In the Australasian region *S. apertura* has been found in Queensland, Australia; Borneo (Sarawak), Sulawesi, Sumatra, Indonesia; and Papua New Guinea (Brown & Dewhurst 1975).

Discussion.—Variation is slight and there is no sexual dimorphism. *Spodoptera apertura* is very similar in forewing ground color and pattern to *S. marima* of the Neotropics, though the genitalia are quite distinct.

Spodoptera malagasy Viette

Figs. 103, 132, 217–218, 315, 345, 377, 409, 441, 528

Spodoptera leucophlebia malagasy Viette 1967: 540.
Spodoptera malagasy; Brown & Dewhurst 1975: 255; Poole 1989: 924.

Diagnosis.—The forewing ground color is lighter in *S. apertura* than in *S. malagasy*, and the hindwing is light brown (Fig. 217–218). The genitalia are similar.

Description. Adult Male.—*Head:* Basal segment of labial palpus black; median segment black with light brown apex; apical segment black, apex cream. Frons with short scales black and cream; long scales black and cream; lateral spots at eye margin absent; vertex black and cream. Antenna serrate; scape black and cream; flagellum cream.

Thorax: Patagium a mixture of fuscous and pale brown scales with a brown band at two-thirds width bordered by white distal border, a brown lateral spot at one-third width. Basal two-thirds of tegula light brown, brown to white at apex. Mesothorax light brown and white. Underside of thorax white. Prothoracic femur fuscous and white; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and light brown, subapical spot pale fuscous; tarsal segment 1 cream, 2 fuscous and cream with cream apical ring, tarsal segments 3–5 fuscous. Mesothoracic femur brown and cream; tibia brown (with a few cream scales), inner spur less than twice length of outer spur, spurs completely scaled; tarsal segments fuscous with cream apical rings.

Metathoracic femur fuscous (with a few white scales); tibia fuscous and cream; tarsal segments fuscous with cream apical rings.

Forewing: Length, 12–16 mm; ground color brown; basal line black; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line pale brown bordered by black, indistinct; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique trapezoid, cream, with a brown center, bordered by thin black lines; reniform spot cream outlined in black, center light brown with a white median line; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 and down vein CuA2 to postmedial line; postmedial line black, indistinct, from just below costa to posterior margin, wavy (can consist of only a few scales); postmedian band undifferentiated; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches in postmedian area (can be reduced in size); subterminal line a light brown band bordered by white (can be bordered by cream); apex lacking a white patch; dark brown square spots along outer margin; fringe dark brown. Underside ground color pale gray; outer margin spots absent; reniform spot absent.

Hindwing: Ground color light brown; fringe white. Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin spots absent; no spot on underside.

Abdomen: Dorsum pale gray; venter brown and cream; disto-lateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 315, 345). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla slender, elongate; apex pointed and hooked; curves along longitudinal plane of valve; extending beyond apex of valve (Figs. 315, 345). Clasper proper absent. Clavus a minute round projection. Sacculus broadest at base, gradually tapering distally; apex pointed. Valvula narrower than valve; well differentiated from valve, apex free; apex round; indentation absent. Coremata reduced, closely appressed to sacculus; no distinct lobes. Juxta a narrow rectangular band with ventrolateral-lateral projections, median process as wide as base, ventral margin straight with curved sides. Anellus membranous. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch quadrate; short, extending to just beyond apex of aedoeagus; cornuti in form of minute flat granules; lateral cornutal patch absent; dense cornutal patch subapical on vesica; distal cornutus an ovate plate with large spines at apex.

Adult Female.—Essentially as described for male except:

Forewing: Length, 16–17 mm.

Abdomen: Fine dense scales on 8th segment cream.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; a few striae. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; forming greater than a 45 degree angle to vertical axis of corpus bursae.

Larva.—Unknown.

Type material.—*Spodoptera leucophlebia malagasy* Viette. The holotype ♂ [MNHP] is labeled: TYPE; Madagascar, Est district d'Ifanadiana, env de Ranomafana, alt 700m, P. Viette le 28-3-1955; Genitalia ♂, P. Viette, Prép. No. 3508; *Spodoptera leucophlebia malagasy* n. subsp., Holotype P. Viette. Type locality: Est district d'Ifanadiana, env de Ranomafana, Madagascar. Allotype ♀ [MNHP] is labeled: Allotype, Madagascar Est, district d'Ifanadiana, env de Ranomafana alt 700m, P. Viette le 30-3-1955; *Spodoptera leucophlebia malagasy* n. subsp., Allotype P. Viette. Type locality: East district of Ifanadiana, vicinity of Ranomafana, Madagascar.

Material Examined.—Specimens were examined from the following countries: Madagascar.

Distribution (Fig. 528).—Only known from Madagascar.

Discussion.—There appears to be slight variation and no sexual dimorphism. Viette (1967) described *S. malagasy* as a subspecies of *S. apertura*. Brown & Dewhurst (1975) elevated it to species rank based on the difference in coloration of the hindwing, the larger size, and the slightly different shape of the male antennal segments.

***Spodoptera compta* (Walker)**

Figs. 107, 219–220, 316, 346, 378, 410, 442, 529

Laphygma compta Walker 1869: 31.
Spodoptera compta; Hampson 1909: 255; Draudt 1926: 256; Poole 1989: 922.

Diagnosis.—Could possibly be confused with *S. evanida*, but *S. compta* is lighter in ground color and posterior half of postmedian line is outlined in white (Figs. 219–220).

Description. Adult Male.—*Head:* Basal segment of labial palpus light brown speckled with rufous and white scales; median segment light brown speckled with rufous and white scales; apical segment light brown speckled with rufous and white scales. Frons with short scales cream; long scales cream; lateral spots at eye margin absent; vertex light brown. Antenna filiform; scape light brown; flagellum cream annulated brown, becoming completely cream toward apex.

Thorax: Patagium light brown. Tegula light brown. Mesothorax light brown. Underside of thorax cream. Prothoracic femur light brown and white; tibia with lateral scale tufts not extending beyond first tarsal segment, light brown and white, subapical spot fuscous (faint); tarsal segments 1–2 cream, 3–5 pale fuscous with cream apical rings. Mesothoracic femur light brown and cream; tibia light brown and cream, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments 1–3 rufous and cream, 4–5 pale fuscous and rufous with cream apical rings. Metathoracic femur rufous and cream; tibia rufous and cream; tarsal segments 1–5 pale fuscous and cream with cream apical rings.

Forewing: Length, 12 mm (n=2); ground color rufous; basal line absent; longitudinal black dash at base absent; antemedial line absent; claviform spot absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; orbicular spot oval, light brown; reniform spot absent; all longitudinal veins faintly outlined in pale brown and a few white scales from discal cell to outer margin; postmedial line pale brown from M1 to anal vein outlined with white from M3 to anal vein; subterminal line absent; apex lacking a white patch; spots along outer margin absent; fringe rufous. Underside ground color white with cream on leading edge and along veins; reniform spot absent.

Hindwing: Ground color white; no other markings, immaculate; fringe white. Underside ground color white; costal cells C and Sc cream speckled with rufous scales; outer margin spots absent; no spot on underside.

Abdomen: Dorsum cream; venter cream (speckled with rufous scales); disto-lateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, well sclerotized. Tegumen with lateral swellings at basal two-thirds. Costa convex (Figs. 316, 346). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus curved at costal apex, outer margin straight. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla short, thumb-shaped lobe, apex round (Figs. 316, 346). Clasper proper with apex round, curved toward sacculus (Figs. 316, 346). Clavus absent. Sacculus broad to half its length, tapering distally; apex pointed. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation absent. Coremata reduced, closely appressed to sacculus; no distinct lobes. Juxta quadrate with lateral third distinct, ventral margin an inverted V-shape. Anellus with minute granules. Vinculum round. Aedoeagus straight; coecum smaller in diameter than shaft; patch of various sized robust spines on apex of membranous sheath surrounding aedoeagus.

Adult Female.—Essentially as described for male except:

Genitalia: Ventral plate of ostium bursa wider than high; distal margin with a single median projection; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); unsclerotized. Appendix bursae membranous. Corpus bursae bulbous, length less than twice width; striate convolutions.

Signum in apical half of corpus bursae; moderately elongate, length between 0.66–1.1 mm; almost vertical.

Larva.—Unknown.

Type material.—*Laphygma compta* Walker. The holotype ♂ [BMNH] is labeled: Type; Norris Coll., 73-41; Peru; *compta;* Noctuidae genitalia slide No. 3474 ♂. Type locality: Peru.

Material Examined.—Specimens were examined from the following country: Peru.

Distribution (Fig. 529).—Known from Peru.

Discussion.—Only three specimens are known, all at the BMNH. No precise locality information is known as the locality labels only read "Peru".

Spodoptera eridania (Stoll)

Figs. 21, 23, 34, 37, 42, 139, 146–148, 221–223, 317, 347, 379, 411, 443, 477–479, 529

Phalaena eridania Stoll, *in* Cramer 1782: 133, plate 358, figs. E, F (1781); index p. 249 (1782).
Noctua linea Fabricius 1794: 106.
Phalaena phytolaccae J.E. Smith 1797: 193, plate 97; Walker 1856: 195.
Xylomyges putrida Guenée, *in* Boisduval & Guenée 1852a: 148.
Xylomyges amygia Guenée, *in* Boisduval & Guenée 1852a: 149.
Leucania externa Walker 1856: 114.
Xylina bipunctata Walker 1857b: 629.
Xylina inquieta Walker 1857b: 632.
Prodenia strigifera Walker 1858: 1678.
Laphygma peruviana Walker 1865a: 650; [Synonymized by Todd & Poole 1980: 733).
Laphygma communicata Walker 1869: 31; [Synonymized by Todd & Poole 1980: 733).
Actinotia derupta Morrison 1875: 62.
Prodenia ignobilis Butler 1878: 485.
Leucania nigrofasciata Hulst 1881: 77.
Laphygma eridania; Druce 1889: 268.
Callierges recondita Möschler 1890: 140.
Prodenia eridania; Smith 1891: 45; Smith 1893: 169; Grote 1895: 42; Dyar 1903: 123; Barnes & McDunnough 1917: 67; McDunnough 1938: 96; Richards 1941: 238; Linsley & Usinger 1966: 160.
Xylomyges eridania; Hampson 1909: 271.
Spodoptera eridania; Hayes 1975: 174; Todd & Poole 1980: 730; Franclemont & Todd 1983: 141; Goater 1983: 278; Poole 1989: 923; Poole & Gentili 1996: 774.

Diagnosis.—Forewing with a short longitudinal black dash at base of posterior margin, which can be faint in worn specimens (Figs. 221–223). Reniform spot round, black (Fig. 222), but usually very faint, or can be modified into a distinct longitudinal black streak extending to wing margin (Fig. 223). Streaking of forewing heavier and browner than in *S. albula.* Male genitalia with valve narrower (Figs. 317, 347) than in *S. albula* (Figs. 318, 348) or *S. ochrea* (Figs. 319, 349). Female genitalia with a bifurcate median projection on distal margin of ventral plate of ostium bursa (Fig. 443); fine dense hairs on 8th segment whitish.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment cream mixed with rufous scales. Frons with short scales cream; long scales cream; lateral spots at eye margin rufous; vertex cream to rufous. Antenna filiform; scape cream; flagellum cream.

Thorax: Patagium light brown flecked with black, median transverse band white. Tegula light brown (tips of a few scales black). Mesothorax with light brown and brown scales, some tipped white. Underside of thorax white. Prothoracic femur light brown to fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, fuscous and rufous, subapical spot absent; first tarsal segment light brown mixed with cream, remainder light brown, cream apical rings present only on tarsal segments 1 and 2. Mesothoracic femur cream and rufous; tibia cream and rufous, inner spur more than twice length of outer spur, spurs completely scaled, first tarsal segment light brown mixed with cream, remainder light brown, apical rings on tarsal segments 1–4. Metathoracic femur cream and rufous; tibia cream and rufous; first tarsal segment light brown mixed with cream, remainder light brown, apical rings on tarsal segments 1–4.

Forewing: Length, 13–15.5 mm; ground color cream; basal line absent; indistinct short longitudinal black dash at base along posterior margin; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line absent; claviform spot absent; basal scale patch absent; indistinct gray patch covering anal cell and half of cell CuA2; oblique brown mark from fifth outer marginal spot to vein CuA2; curved white line from antemedial line to postmedial line absent; orbicular spot absent; reniform spot

round, black, or can include a black longitudinal streak ending at outer margin (can be faint to absent in some specimens); white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line absent; postmedian band undifferentiated; black scale patches in middle of cells in postmedian area absent; subterminal line absent; apex lacking a white patch; minute black spots along outer margin; fringe brown. Underside ground color cream; outer margin with black spots; reniform spot round, black, or in the form of a longitudinal streak dark gray and not extending to outer margin.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales; fringe white. Underside ground color white; costal cells C and Sc cream speckled with brown scales; outer margin with gray triangular spots in middle of cells Sc to CuA1 (indistinct); no spot on underside.

Abdomen: Dorsum pale gray; venter cream and rufous; disto-lateral black spots on sternites; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; maintaining width throughout three-fourths length, narrowing to pointed apex; setae absent or few. Scaphium elongate, well sclerotized. Tegumen with a pair of projecting arms on upper third. Costa convex (Figs. 317, 347). Costal process short, wide. Cucullus curved at costal apex, outer margin straight. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla a short, thumb-shaped lobe, apex round (Figs. 317, 347). Clasper proper apex pointed, curved toward costa (Figs. 317, 347). Clavus absent. Sacculus broad on basal half, tapering distally; apex pointed. Valvula narrower than valve; well differentiated from valve, apex free; apex round; indentation absent. Coremata moderately elongate, approximately 0.5 or less length of valve; composed of a single lobe. Juxta a narrow rectangular band, median process wide as base and constricted near apical third, ventral margin a broad inverted V-shape. Anellus with a sclerotized plate with lateral spines. Vinculum round. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving dorsally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a wide ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon, divided basally; a mixture of short, conical, and more elongate slender spines; dense cornutal patch at apex of vesica; distal cornutus absent.

Adult Female.—Essentially as described for male except:

Forewing: Length, 13–16 mm.

Abdomen: Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa wider than high; distal margin with a bifurcate median projection; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae membranous. Corpus bursae elongate, length greater than twice width; striate convolutions. Signum at middle of corpus bursae; elongate, length greater than 1.15 mm; forming less than a 45 and greater than a 30 degree angle to vertical axis of corpus bursae, oriented left to right.

Larva.—See description, p. 105.

Type material.—*Phalaena eridania* Stoll. The type material was not located during this study and is considered lost. The neotype ♂ [USNM, **here designated**] is labeled: Archbold Biol. Sta.,; L. Placid, Highlands; County, Florida; 8 Jan. 1983; D. C. Ferguson. USNM ENT 00057649. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 222. Type locality: Archbold Biological Station, Lake Placid, Highlands County, Florida.

Noctua linea Fabricius. The type is apparently lost. Type locality: "Americae Meridionalis Insulis" [West Indies].

Phalaena phytolaccae J.E. Smith. The type is apparently lost. Type locality: Georgia, USA.

Xylomyges putrida Guenée. The holotype ♂ [BMNH] is labeled: Guadeloupe. Type locality: Guadeloupe.

Xylomyges amygia Guenée. The lectotype [BMNH, **here designated**] is labeled: Nova Friburgo, Brazil. The lectotype is designated to ensure nomenclatural stability in this confusing group of species. Type locality: Nova Friburgo, Brazil. The following syntypes become paralectotypes: (1) Label data: Brasil Becker; (3) Label data: Brasil; (4) Label data: Fribourg.

Leucania externa Walker. The holotype ♀ [BMNH] is labeled: St. Vincent, 39-7-17, 70; Noc-

tuidae genitalia slide No. 1494 ♀. Type locality: St. Vincent.

Xylina bipunctata Walker. The type(s) are deposited in University Museum, Oxford University, Oxford. Type locality: Brazil.

Xylina inquieta Walker. The holotype ♀ [BMNH] is labeled: [No locality label] *Xylina inquieta;* Noctuidae genitalia slide No. 1493 ♀. Type locality: unknown.

Prodenia strigifera Walker. The holotype [BMNH] is labeled: Amazonas, Ega, 58-6. Type locality: Téfe, Brazil.

Laphygma peruviana Walker. The ♀ lectotype [BMNH, **here designated**] is labeled: [No locality label]; Syntype, Norris Coll., 73-41; *Leucania, peruviana.* The lectotype is designated to ensure nomenclatural stability in this confusing group of species. Type locality: Peru.

Laphygma communicata Walker. The ♂ lectotype [BMNH, **here designated**] is labeled: Syntype, Norris Coll. 73-41; Peru; *communicata;* Noctuidae genitalia slide No. 1500 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species. Type locality: Peru.

Actinotia derupta Morrison. The type(s) are deposited in Michigan State University, East Lansing, Michigan. Type locality: Texas, USA.

Prodenia ignobilis Butler. The ♂ lectotype [BMNH, **here designated**] is labeled: Jamaica, J. J. Bowrey, 78-19; *Prodenia ignobilis,* Butler Type; Noctuidae genitalia slide No. 1498 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species.Type locality: Jamaica.

Leucania nigrofasciata Hulst. The holotype ♀ [AMNH] is labeled: Fla., USA. Collection G.D. Hulst; *Leucania, nigrofasciata,* Type, Hulst. Type locality: Tallahassee, Florida, USA.

Callierges recondita Möschler. The 2 ♀ syntypes are deposited in Museum für Naturkunde der Humboldt University, Berlin. Type locality: Puerto Rico.

Material Examined.—Specimens were examined from the following countries: Argentina, Bahamas, Bermuda, Brazil, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, El Salvador, French Guiana, Guadeloupe, Guatemala, Guyana, Honduras, Jamaica, Mexico, Panama, Paraguay, Peru, Puerto Rico, St. Lucia, Surinam, United States, Venezuela.

Distribution (Fig. 529).—This species occurs in the southeastern United States from Maryland south to Florida and west to Kentucky and Texas. Strays have been reported in northeastern Ohio (Rings *et al.* 1992). In the Neotropics it ranges from Mexico, throughout the Caribbean, and south through Central America to Argentina.

Discussion.—*S. eridania* is quite variable as is evident by the number of synonyms. The forewing ground color is most commonly cream, but can become gray. The pattern on the forewing can also vary, specimens can have a faint or obscure reniform spot, a distinct reniform spot, or an elongate horizontal bar extending from the reniform spot to wing margin. Sexual dimorphism is not evident in *S. eridania.*

Spodoptera albula (Walker)

Figs. 26, 30, 39, 53, 60, 71, 84, 93, 106, 115, 144, 153, 224–226, 304, 318, 348, 380, 412, 444, 480–482, 530

Xylina albula Walker 1857b: 629.

Laphygma orbicularis Walker 1857b: 719 [preoccupied, a secondary junior homonym of *Caradrina orbicularis* Walker]; Druce 1889: 267; [synonymized by Poole 1989: 925].

Laphygma caudata Walker 1869: 32; [synonymized by Poole 1989: 922].

Spodoptera sunia; Levy & Habeck 1976: 585; Todd & Poole 1980: 733; Franclemont & Todd 1983: 141. (This is the species previously identified as "*Spodoptera sunia* Guenée". The real *Xylomyges sunia* Guenée 1852 is actually the species currently known as *Neogalea esula* Druce.)

Spodoptera albula; Poole 1989: 922; Poole & Gentili 1996: 773.

Diagnosis.—Forewing with a short black longitudinal dash at base of Cu vein (Figs. 224–226). Reniform spot round and black (Fig. 225) or can be faint to absent (Figs. 224, 226). Ground color more pale gray with streaking black compared to a more brown ground color with brown streaking in *S. eridania.* Male genitalia with a pair of projecting arms on upper third of tegumen (Fig. 37). Valve wider than in *S. eridania* (compare Figs. 347 and 348). Female genitalia with a large median projection on posterior margin of ventral plate of ostium bursa (Fig. 444); fine dense scales on 8th segment gray.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band vari-

ably mixed with rufous scales; apical segment cream mixed with rufous scales. Frons with short scales white (with a few rufous scales); long scales white and brown; lateral spots at eye margin brown; vertex pale rufous. Antenna filiform; scape white and rufous; flagellum white and rufous.

Thorax: Patagium with light brown scales tipped white, a black transverse band at one-third width. Tegula light brown and white. Mesothorax light brown. Underside of thorax white. Prothoracic femur rufous and fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; tarsal segments 1–2 cream and rufous, segments 3–4 fuscous, segment 5 fuscous with cream apical ring. Mesothoracic femur cream and rufous; tibia cream and rufous, inner spur more than twice length of outer spur, mediolateral surface devoid of scales on large spur; first tarsal segment cream and rufous, remainder fuscous basally, rufous medially with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; first tarsal segment cream and rufous, remainder fuscous basally, rufous medially with cream apical rings.

Forewing: Length, 10–14.5 mm; ground color pale gray to cream; basal line absent; short longitudinal black dash at base of Cu vein; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line absent; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot absent; reniform spot absent to round, black; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line absent; postmedian band undifferentiated; black scale patches in middle of cells in postmedian area absent; subterminal line absent; apex lacking a white patch; minute black spots along outer margin; fringe pale gray to gray. Underside ground color light brown to pale gray; outer margin with black spots; reniform spot gray.

Hindwing: Ground color white; faint black spots along outer margin; fringe white. Underside ground color white; costal cells C and Sc cream speckled with rufous scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray; venter cream and rufous; disto-lateral black spots on sternites (indistinct); 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, well sclerotized. Tegumen with a pair of projecting arms on upper third. Costa convex (Figs. 318, 348). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus broadly rounded. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla short, thumb-shaped lobe, apex round. Clasper proper apex round, curved toward sacculus (Figs. 318, 348). Clavus absent. Sacculus broad in basal half, tapering distally; apex pointed. Valvula narrower than valve; well differentiated from valve, apex free; apex produced and curved toward costa; indentation absent. Coremata moderately elongate, approximately 0.5 or less length of valve; composed of a single lobe. Juxta a narrow rectangular band, median process wide as base and constricted near apical third, ventral margin a broad inverted V-shape. Anellus with a patch of enlarged spines at apex of aedoeagus. Vinculum round. Aedoeagus straight; coecum smaller in diameter than shaft; patch of various sized robust spines on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a wide ribbon; elongate, extending to beyond middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a wide elongate ribbon; composed of short, conical spines; dense cornutal patch at apex of vesica; distal cornutus absent.

Adult Female.—Essentially as described for male except:

Forewing: Length, 12–16 mm.

Abdomen: Fine dense scales on 8th segment gray.

Genitalia: Ventral plate of ostium bursa wider than high; distal margin with a single median projection; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae membranous. Corpus bursae elongate, length greater than twice width; smooth. Signum in apical half of corpus bursae; moderately elongate, length between 0.66–1.1 mm; forming less than a 30 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 106.

Type material.—*Xylina albula* Walker. The ♂ lectotype [BMNH, **here designated**] is labeled: St. Domingo, Tweedie, 55-1; *Xylina albula*; Noctuidae genitalia slide No. 4013 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species. Type locality: Santo Domingo, Dominican Republic. The following syntypes become paralectotypes: (1) ♂, Label data: St. Domingo, Tweedie, 55-1. (2) ♂, Label data: Honduras, Dyson, 45-123. (3) ♀, Label data: [No locality label] 48-58.

Laphygma orbicularis Walker. The ♀ lectotype [BMNH, **here designated**] is labeled: St. Domingo, Tweedie, 55-1; *Laphygma orbicularis*; Noctuidae genitalia slide No. 4014 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of species. Type locality: Santo Domingo, Dominican Republic. The following syntype becomes a paralectotype: ♀, Label data: St. Domingo, Tweedie, 55-1.

Laphygma caudata Walker. The holotype ♂ [BMNH] is labeled: [No locality label] Norris Coll., 73-41; *caudata;* Noctuidae genitalia slide No. 4012 ♂.Type locality: unknown.

Material Examined.—Specimens were examined from the following countries: Antigua, Argentina, Bahamas, Barbados, Belize, Brazil, British Virgin Islands, Cayman Islands, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, El Salvador, French Guiana, Grenada, Guatemala, Guyana, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Paraguay, Puerto Rico, St. Croix, St. Lucia, St. Vincent, United States, Venezuela.

Distribution (Fig. 530).—This species is distributed from Florida and southern Texas, throughout the Caribbean, Central America, and from Venezuela south to Paraguay and southern Brazil.

Discussion.—The reniform spot of the forewing and the black mid-wing bar from the end of the discal cell to outer margin of the forewing can be distinct to absent. Sexual dimorphism is not evident.

Spodoptera albula was previously identified as "*Spodoptera sunia* Guenée". The original combination, *Xylomyges sunia* Guenée (1852a), is actually the species currently known as *Neogalea esula* Druce, which is a synonym of *Neogalea sunia* Guenée. *Laphygma orbicularis* Walker is a synonym of *S. albula* and a secondary junior homonym of *Caradrina orbicularis* Walker, which is a synonym of *S. cilium* (Poole 1989).

Spodoptera ochrea (Hampson)

Figs. 36, 61, 99, 227–229, 319, 349, 381, 413, 445, 530

Xylomyges ochrea Hampson 1909: 273.
Spodoptera ochrea; Todd & Poole 1980: 733; Poole 1989: 924.

Diagnosis.—Forewing streaking much lighter than in *S. albula* and *S. eridania.* Ground color cream. Reniform spot pale gray and indistinct (Figs. 227–229). Male genitalia lacking a pair of projecting arms on upper third of tegumen (Fig. 36). Female genitalia with median projection of ventral plate of ostium bursa shorter than in *S. albula,* and with a broadly round distal margin (Fig. 445); fine dense scales on 8th segment black.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with a few rufous scales; median segment cream variably mixed with rufous and black scales and mixed with black and brown scales in basal half, cream apically; apical segment cream. Frons with short scales white; long scales cream and rufous, or light brown; lateral spots at eye margin rufous (can coalesce into a bar); vertex white (speckled with brown). Antenna filiform; scape white; flagellum white.

Thorax: Patagium cream to light brown (a few specks of black in some specimens). Tegula cream to light brown (a few specks of black in some specimens). Mesothorax cream. Underside of thorax white. Prothoracic femur cream, fuscous, and rufous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream (some scales tipped with a combination of fuscous and rufous), subapical spot absent; tarsal segments cream. Mesothoracic femur cream; tibia cream and rufous, inner spur more than twice length of outer spur, mediolateral surface devoid of scales on large spur; tarsal segments cream. Metathoracic femur cream; tibia cream and rufous; tarsal segments cream.

Forewing: Length, 11.5–14 mm; ground color cream; basal line absent; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line absent; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique

brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot round, white, very faint, with a few brown scales in center; reniform spot pale gray, indistinct; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line absent; postmedian band undifferentiated; black scale patches in middle of cells in postmedian area absent; subterminal line absent; apex lacking a white patch; minute black spots along outer margin; fringe pale gray to buff. Underside ground color white with cream on leading edge and along veins; outer margin with black spots; reniform spot darker, indistinct.

Hindwing: Ground color white; no other markings, immaculate; fringe white. Underside ground color white; costal cells C and Sc white speckled with gray scales; no spot on underside.

Abdomen: Dorsum white to cream; venter cream and gray; disto-lateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen with lateral swellings at basal two-thirds. Costa convex (Figs. 319, 349). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus broadly rounded. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla short, triangular shaped lobe, apex round. Clasper proper apex round, curved toward sacculus (Figs. 319, 349). Clavus absent. Sacculus broad to half its length, tapering distally; apex pointed. Valvula narrower than valve; well differentiated from valve, apex free; apex produced and curved toward costa; indentation absent. Coremata moderately elongate, approximately 0.5 or less length of valve; composed of a single lobe. Juxta a narrow rectangular band, median process wide at base and constricted near apical third, ventral margin a broad inverted V-shape. Anellus with a patch of enlarged spines at apex of aedoeagus. Vinculum round. Aedoeagus straight; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a wide ribbon; elongate, extending beyond middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a wide elongate ribbon; composed of short, conical spines; dense cornutal patch at apex of vesica; distal cornutus absent.

Adult Female. Essentially as described for male except:

Forewing: Length, 13–16.5 mm.

Abdomen: Fine dense scales on 8th segment gray.

Genitalia: Ventral plate of ostium bursa wider than high; distal margin with a single median projection; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae moderately elongate (length 2–3 times width); completely sclerotized. Appendix bursae membranous. Corpus bursae bulbous, length less than twice width; a few striae. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; almost vertical.

Larva.—Unknown.

Type material.—*Xylomyges ochrea* Hampson. The ♂ lectotype [BMNH, **here designated**] is labeled: Peru, Callao, 15-XI-82 -11 II 83, J J Walker; Noctuidae genitalia slide No. 1499 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 227. Type locality: Callao, Peru. The following syntype becomes a paralectotype: Label data: Peru, Callao, J J Walker, 84-72.

Material Examined.—Specimens were examined from the following countries: Ecuador, Peru.

Distribution (Fig. 530).—Known only from Ecuador and Peru.

Discussion.—The forewing ground color varies slightly from cream to pale gray. The reniform spot is usually faint or can be absent. Sexual dimorphism is not evident.

A field-collected larva was reared from asparagus in Peru as part of a preclearance program to identify Lepidoptera associated with asparagus imported into the United States (Pogue and Passoa 2000). Additional plant hosts include cotton (Gonzalez 1978), tobacco, and potato in Peru (Valencia & Valdivia 1973).

Spodoptera exempta (Walker)

Figs. 45, 62, 69, 125, 137, 230–234, 320, 350, 382, 414, 446, 483–485, 531

Agrotis exempta Walker 1857a: 355.
Prodenia bipars Walker 1857b: 724.

Prodenia ingloria Walker 1858: 1679.
Laphygma exempta; Hampson 1909: 261; Warren *in* Seitz 1914a: 322.
Prodenia metriodes Bethune-Baker 1911: 511. **New synonym.**
Spodoptera exempta; Brown & Dewhurst 1975: 243; Sugi 1982: 764; Holloway 1989: 136; Poole 1989: 923; Edwards 1996: 324.

Diagnosis.—Color and pattern most similar to *S. umbraculata,* but the male of *S. exempta* has filiform antenna (Fig. 18). Forewing ground color gray to light brown, orbicular spot oval, white, outlined in black. Male genitalia with clasper proper elongate, bent at middle at almost a right angle, well below apex of valve (Figs. 320, 350). Ampulla a minute lobe at base of clasper proper (Fig. 62) Female genitalia with distal margin of ventral plate of ostium bursa convex (Fig. 446); fine dense scales on 8th segment black.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment black mixed with cream scales; apical segment a mixture of cream, brown, and black scales. Frons with short scales cream (can be suffused with gray); long scales cream (can be suffused gray); lateral spots at eye margin black; vertex white to cream. Antenna filiform; scape cream; flagellum cream (annulated brown).

Thorax: Patagium basal half gray, apical half lighter. Tegula light brown (gray scales on lateral margin). Mesothorax light brown. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, rufous, fuscous, and cream, subapical spot absent; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur fuscous and cream; tibia cream, rufous, and fuscous; inner spur less than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and fuscous; tibia cream and fuscous; first tarsal segment cream mixed with fuscous, segments 2–5 fuscous with cream apical rings.

Forewing: Length, 10–14 mm; ground color gray to light brown; basal line black; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line black; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, cream, with buff to brown center, outlined in black; reniform spot cream outlined in black, apex with a white V-shaped mark, center black; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line black, from just below costa to posterior margin, wavy; postmedian band with an indistinct, round, black spot along subterminal line; black scale patches in middle of cells M1 to M3, with or without faint patches in R5 and CuA1 in postmedian area; subterminal line white, indistinct; apex with a white patch; black triangular-shaped spots along outer margin; fringe gray. Underside ground color pale gray; outer margin with black spots; reniform spot darker, indistinct.

Hindwing: Ground color white suffused with light brown; apex, outer margin, and veins with light brown scales; fringe light brown to pale gray at apex and median line, becoming white toward anal veins. Underside ground color white; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray; venter cream and gray; disto-lateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa sinuate (Figs. 320, 350). Costal process a minute knob; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex round; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla a minute lobe at base of clasper proper (Fig. 62). Clasper proper slender, elongate; apex pointed and hooked; curved toward sacculus; extends to well below apex of valve (Figs. 62, 320, 350). Clavus absent. Sacculus narrow, width less than 0.2 length, tapering distally; apex pointed. Valvula wider than valve; well differentiated from valve, apex free; apex round; indentation with

base of ventral margin near apex of sacculus, slightly curved. Coremata moderately elongate, approximately 0.5 or less length of valve; composed of a single lobe. Juxta a narrow elliptical band, median process triangular-shaped, ventral margin concave. Anellus membranous. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving dorsally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a wide ribbon; short, extending to just beyond apex of aedoeagus; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon; composed of large spines; dense cornutal patch subapical on vesica; distal cornutus many large spines.

Adult Female.—Essentially as described for male except:

Forewing: Length, 13–15.5 mm. Ground color gray; basal line black; antemedial line black; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; reniform spot cream outlined in black, apex with a white V-shaped mark, center black; postmedial line black, from just below costa to posterior margin, wavy; apex lacking a white patch; black triangular-shaped spots along outer margin; fringe gray. Underside ground color pale gray; outer margin with black spots; reniform spot darker, indistinct.

Abdomen: Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa wider than high; distal margin convex; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae moderately elongate (length 2–3 times width); completely sclerotized. Appendix bursae membranous. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum at middle of corpus bursae; elongate, length greater than 1.15 mm; almost vertical.

Larva.—See description, p. 106.

Type material.—*Agrotis exempta* Walker. The holotype ♂ [BMNH] is labeled: Holotype; [Locality unknown]; Noc. Geni. Slide No. 585 ♂. Type locality: unknown.

Prodenia bipars Walker. The holotype ♀ [BMNH] is labeled: Holotype, Queensland, Moreton B, S. Diggles, 57-130. Type locality: Moreton Bay, Queensland, Australia.

Prodenia ingloria Walker. The holotype ♂ [BMNH] is labeled: Holotype Queensland, Moreton B, S. Diggles, 57-130. Type locality: Moreton Bay, Queensland, Australia.

Prodenia metriodes Bethune-Baker. The holotype ♂ [BMNH] is labeled: Holotype, N. Nigeria, D. Cator; Noc. gen. Slide 3807 ♂. Type locality: N. Nigeria.

Material Examined.—Specimens were examined from the following countries: Aldabra Atoll, Angola, Australia, Botswana, Cameroon, Cook Islands, Democratic Republic of the Congo, Djibouti, Ethiopia, Ghana, Guinea, Indonesia, Ivory Coast, Kenya, Kiribati, Line Islands, Madagascar, Malawi, Malaysia, Marshall Islands, Mozambique, Namibia, Nigeria, Papua New Guinea, Philippines, Saudi Arabia, Senegal, Sierra Leone, Singapore, Solomon Islands, South Africa, Sri Lanka, Sudan, Sumatra, Tanzania, Thailand, Uganda, United States (Hawaii), Yemen, Zimbabwe.

Distribution (Fig. 531).—*Spodoptera exempta* is widely distributed in southern Europe, the islands of the Mediterranean, the Ethiopian Region, Aldabra Island in the Indian Ocean, the Australasian Region, and throughout the South Pacific to Hawaii.

Discussion.—Specimens can be variable across their geographic range. Individuals from the South Pacific and Hawaii are lighter in ground color than specimens from Africa and Asia. *Spodoptera exempta* is sexually dimorphic with the female having a dark gray ground color and lacking the broad light colored mark running obliquely from the orbicular spot.

Poole (1989) listed *Prodenia metriodes* as a synonym of *S. littoralis*. The type of *P. metriodes* is referable to *S. exempta*.

Spodoptera mauritia (Boisduval)

Figs. 22, 24, 31, 50, 55, 126, 169–171, 235–248, 321, 351, 383, 415, 447, 464–470, 486–488, 532

Hadena mauritia Boisduval 1833: 92.

Spodoptera acronyctoides Guenée *in* Boisduval & Guenée 1852a: 154; Walker 1856: 187.

Spodoptera acronyctiformis Guenée *in* Boisduval & Guenée 1852b: 399 [An unnecessary replacement name for *Spodoptera acronyctoides* Guenée]; Poole 1989: 922 [placed in synonymy].

Spodoptera filum Guenée *in* Boisduval & Guenée 1852a: 155; Walker 1856: 187.

Spodoptera nubes Guenée *in* Boisduval & Guenée 1852a: 155; Walker 1856: 186; [synonymized by Hampson 1894: 248].

Prodenia infecta Walker 1856: 196; Walker 1856: 196.

Prodenia insignata Walker 1856: 197.
Agrotis transducta Walker 1857a: 344.
Prodenia permunda Walker 1857b: 723.
Agrotis aliena Walker 1865a: 694.
Agrotis bisignata Walker 1865a: 702
Laphygma squalida Walker 1865a: 651.
Prodenia venustula Walker 1865a: 654.
Agrotis submarginalis Walker 1865a: 699.
Hadena obliqua Walker 1865b: 736.
Prodenia nubes; Cotes & Swinhoe 1888: 326; Swinhoe 1890: 227.
Hermonassa formosana Matsumura *in* Shiraki 1913: 509.
Euxoa ogasawarensis Matsumura 1926: 6, pl. 1, fig. 19.
Spodoptera mauritia; Walker 1856: 186; Warren *in* Seitz 1914a: 321; Fletcher 1956: 215; Brown & Dewhurst 1975: 247; Holloway 1976: 12; Sugi 1982: 764; Holloway 1989: 133; Poole 1989: 924; Edwards 1996: 324.

Diagnosis.—Most similar to *S. triturata*, forewing ground color of *S. mauritia* darker and pattern less distinct. Forewing with orbicular spot oval, cream, with buff to brown center. Male genitalia with ampulla elongate, shorter than in *S. triturata*; coremata more triangular-shaped (compare Figs. 351 and 352). Female ventral plate of ostium bursa with distal margin straight (Fig. 447); corpus bursae round and more distinct from ductus bursae than in *S. triturata* (compare Figs. 415 and 416); fine dense scales on 8th segment.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; black, variably mixed with brown and cream, apex cream (lightly speckled with brown); apical segment black mixed with a few cream scales. Frons with short scales cream; long scales cream to rufous; lateral spots at eye margin black; vertex cream and light brown. Antenna filiform; scape brown; flagellum brown (annulated black in basal third).

Thorax: Patagium light brown with brown scales forming indistinct basal and median bands. Tegula brown. Mesothorax brown. Underside of thorax cream. Prothoracic femur fuscous and cream; tibia with lateral scale tufts extending beyond first tarsal segment, rufous, fuscous, and cream, subapical spot absent; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur fuscous and cream; tibia fuscous and cream, inner spur less than twice length of outer spur; mediolateral surface broadly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings (faint on segment 4). Metathoracic femur fuscous and cream; tibia cream, rufous, and fuscous; tarsal segments fuscous with cream apical rings.

Forewing: Length, 12.5–15 mm; ground color gray; basal line black (indistinct); R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line black (indistinct); claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, cream, with buff to brown center, outlined in black; reniform spot round, black; white scales at junction of veins M3 and CuA1 which can extend to orbicular spot; postmedial line black, indistinct, from just below costa to posterior margin, wavy; postmedian band with an indistinct, round, black spot along subterminal line; black scale patches in middle of cells in postmedian area absent; subterminal line white, indistinct; apex lacking a white patch; black trapezoidal-shaped spots along outer margin; fringe gray. Underside ground color pale gray; outer margin with black spots; reniform spot absent.

Hindwing: Ground color white; apex, outer margin, and veins with light brown scales; fringe light brown to pale gray at apex and median line, becoming white toward anal veins. Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin suffused with gray scales and with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray; venter rufous; disto-lateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus evenly curved; wider at middle than at base; setae numerous. Scaphium weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa sinuate (Figs. 321, 351). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex round; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a decurved apex; curved toward sac-

culus; extending to well below apex of valve (Figs. 321, 351). Clasper proper absent. Clavus a minute round projection. Sacculus narrow, width less than 0.2 length, tapering distally; apex pointed. Valvula wider than valve; well differentiated from valve, apex free; apex round; indentation with base of ventral margin near apex of sacculus, slightly curved. Coremata moderately elongate, approximately 0.5 or less length of valve; composed of a single lobe. Juxta a narrow elliptical band, median process triangular-shaped, ventral margin concave. Anellus with minute granules. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving dorsally; elongate, greater than length of aedoeagus; apicobasal cornutal patch a narrow ribbon; short, extending to just beyond apex of aedoeagus; cornuti in form of minute flat granules; lateral cornutal patch absent; dense cornutal patch absent; distal cornutus a large spine.

Adult Female. Essentially as described for male except:

Thorax: Prothoracic femur fuscous and cream; tibia with lateral scale tufts extending beyond first tarsal segment, fuscous and rufous, subapical spot absent; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur fuscous and cream; tibia fuscous and cream, inner spur less than twice length of outer spur, spurs completely scaled; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and rufous; tibia cream, rufous, and fuscous; tarsal segments fuscous with cream apical rings.

Forewing: Length, 13–18 mm. White scales along R vein and bases of M and CuA veins absent.

Abdomen: Fine dense scales on 8th segment cream. Venter rufous (or cream and gray); distolateral black spots on sternites (indistinct).

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae membranous. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in basal half of corpus bursae; moderately elongate, length between 0.66–1.1 mm; almost vertical.

Larva.—See description, p. 107.

Type material.—*Hadena mauritia* Boisduval. The type material was not located during this study and is considered lost. The neotype ♂ [USNM, **here designated**] is labeled: New Caledonia; near Dumbea; black light; 22 December 1976; Gary F. Hevel. USNM ENT 00065927. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 235. Type locality: near Dumbea, New Caledonia.

Spodoptera acronyctoides Guenée. The holotype ♀ repository is unknown. Type locality: Tahiti, French Polynesia.

Spodoptera filum Guenée. The lectotype ♀ [BMNH, **here designated**] is labeled: syntype, 60.15 EIC; *Spodoptera filum* [hand written]; Noctuidae genitalia slide No. 3819 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 239. Type locality: [probably Java, Indonesia].

Spodoptera nubes Guenée. The lectotype ♂ [BMNH, **here designated**] is labeled: [no locality given], syntype, 60.15 EIC; *Spodoptera nubes* [hand written]; Noctuidae genitalia slide No. 3818 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 242. Type locality: [probably Java, Indonesia].

Prodenia infecta Walker. The holotype ♀ [BMNH] is labeled: Holotype , N. India, L. James, 43-10; *Prodenia infecta;* Noctuidae genitalia slide No. 3820 ♀. Type locality: [Northern] India .

Prodenia insignata Walker. The holotype ♂ is deposited in BMNH. Type locality: India (Northern).

Agrotis transducta Walker. The holotype ♀ [BMNH] is labeled: Holotype, Ceylon, Templeton, 52-62; 91., *Agrotis transducta;* Noctuidae genitalia slide No. 3822 ♀. Type locality: Sri Lanka.

Prodenia permunda Walker. The holotype ♂ [BMNH] is labeled: Holotype, Siam, J.C. Bowring, 56-113; *Prodenia permunda;* Noctuidae genitalia slide No. 3823 ♂. Type locality: Thailand.

Agrotis aliena Walker. The holotype ♀ [BMNH] is labeled: Holotype, Mauritius, 57-140. Type locality: Mauritius.

Agrotis bisignata Walker. The holotype ♀

[BMNH] is labeled: Holotype, Queensland, Moreton B., Diggles, 59-105; Noctuidae genitalia slide No. 3827 ♀. Type locality: Moreton Bay, Queensland, Australia.

Laphygma squalida Walker. The holotype ♂ [BMNH] is labeled: Holotype, N. India, L. James, 43-10; *Laphygma squalida*; Noctuidae genitalia slide No. 3824 ♂. Type locality: Northern India.

Prodenia venustula Walker. The holotype ♂ [BMNH] is labeled: Holotype, S. India, Coimbatoor, M.T. Walhouse, 61-20; *Prodenia venustula*; Noctuidae genitalia slide No. 3825 ♂. Type locality: Coimbatoor, S. India.

Agrotis submarginalis Walker. The holotype ♀ [BMNH] is labeled: Holotype, Java, Horsfield; *Agrotis submarginalis*; Noctuidae genitalia slide No. 3826 ♀. Type locality: Java, Indonesia.

Hadena obliqua Walker. The holotype ♂ [BMNH] is labeled: Holotype, Shanghai, 58-60; Noctuidae genitalia slide No. 3828 ♂. Type locality: Shanghai, China.

Hermonassa formosana Matsumura. The type repository is unknown. Type locality: Taiwan.

Euxoa ogasawarensis Matsumura. The syntypes: 1 ♂, 2 ♀, in Entomological Institute, Hokkaido University, Sapporo. Type locality: Bonin Islands, Ogasawarajima, Japan.

Material Examined.—Specimens were examined from the following countries: American Samoa, Australia, Bahrain, Burma, Christmas Islands, Cocos (Keeling) Islands, Comoro Islands, Cook Islands, Easter Island, Federated States of Micronesia, Fiji, French Polynesia, Guam, Hong Kong, India, Indonesia, Japan, Kiribati, Korea, Madagascar, Malaysia, Maldive Islands, Marshall Islands, Mauritius, Nepal, New Caledonia, Nigeria, Norfolk Island, Northern Marianas, Pakistan, Palau, Papua New Guinea, Philippines, Pitcairn Island, Réunion, Seychelles, Singapore, Solomon Islands, South Africa, Sri Lanka, Taiwan, Tanzania, Thailand, Tonga, United States (Hawaii), Vanuatu, Western Samoa.

Distribution (Fig. 532).—*Spodoptera mauritia* is widely distributed in southern Asia, Australasia, and throughout the Pacific to Hawaii. It occurs in Madagascar, the Seychelles, and Mauritius in the Indian Ocean. Its African distribution is limited to Kenya and Tanzania (Brown & Dewhurst 1975) and from Nigeria and South Africa.

Discussion.—There is some variation in the forewing ground color. Most typically it is gray but can be lighter. Sexual dimorphism occurs in *S. mauritia* with the female lacking the oblique white mark surrounding orbicular spot.

Spodoptera triturata (Walker)

Figs. 40, 49, 127, 249–252, 322, 352, 384, 416, 448, 533

Caradrina triturata Walker 1857a: 295.
Laphygma gratiosa Walker 1865a: 651.
Celaena bisignata Walker 1865a: 679.
Spodoptera triturata; Fletcher 1956: 217; Brown & Dewhurst 1975: 251; Poole 1989: 925.

Diagnosis.—Most similar to *S. mauritia*, but in *S. triturata* forewing ground color lighter and pattern more distinct. Forewing with orbicular spot round, white with brown center, outlined in black. Male genitalia with ampulla longer and coremata narrower at base than in *S. mauritia* (compare Figs. 351 and 352. Female genitalia with distal margin of ventral plate of ostium bursa straight (Fig. 448); corpus bursae bulbous and less distinct from ductus bursae than in *S. mauritia* (compare Figs. 415 and 416); fine dense scales on 8th segment black.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment black, variably mixed with brown and cream, apex cream (lightly speckled with brown); apical segment black mixed with a few cream scales. Frons with short scales brown; long scales brown; lateral spots at eye margin black; vertex brown. Antenna filiform; scape cream; flagellum brown (annulated black in basal third).

Thorax: Patagium light brown mixed with brown and white scales. Tegula light brown (some scales tipped with white and brown). Mesothorax with light brown and brown scales, some tipped white. Underside of thorax cream. Prothoracic femur cream and fuscous; tibia with lateral scale tufts extending beyond first tarsal segment, rufous, fuscous, and cream, subapical spot absent; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur cream and fuscous; tibia cream, rufous, and fuscous, inner spur less than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings. Metatho-

racic femur cream and fuscous; tibia cream and fuscous; tarsal segments fuscous with cream apical rings.

Forewing: Length, 14–16 mm; ground color gray; basal line black (which consists of a few scales); longitudinal black dash at base absent; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line black (indistinct); claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot round, white, with brown center, outlined in black; reniform spot round, black; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line black, indistinct, from just below costa to posterior margin, wavy; postmedian band with an indistinct, round, black spot along subterminal line; black scale patches in middle of cells in postmedian area absent; subterminal line white, indistinct; apex lacking a white patch; black trapezoidal-shaped spots along outer margin; fringe gray. Underside ground color pale gray; outer margin with black spots; reniform spot darker, indistinct.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales. Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1 (can be indistinct to absent); no spot on underside.

Abdomen: Dorsum pale gray; venter rufous (or cream and gray); disto-lateral black spots on sternites absent; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae numerous. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa sinuate (Figs. 322, 352). Costal process an indistinct swelling bearing setae; at base of costa along margin; perpendicular to costa of valve. Cucullus apex round; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a decurved apex; curved toward sacculus; extending to moderately below apex of valve (Figs. 322, 352). Clasper proper absent. Clavus absent. Sacculus narrow, width less than 0.2 length, tapering distally; apex pointed. Valvula wider than valve; well differentiated from valve, apex free; apex pointed; indentation with base of ventral margin near apex of sacculus, slightly curved. Coremata moderately elongate, approximately 0.5 or less length of valve; composed of a single lobe. Juxta a narrow elliptical band, median process triangular-shaped, ventral margin concave. Anellus with minute granules. Vinculum U-shaped with a narrow base. Aedoeagus straight; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving dorsally; elongate, greater than length of aedoeagus; apicobasal cornutal patch a narrow ribbon; short, extending just beyond apex of aedoeagus; cornuti in form of minute flat granules; lateral cornutal patch absent; dense cornutal patch subventrally on vesica; distal cornutus a large spine.

Adult Female.—Essentially as described for male except:

Forewing: Length, 15–17 mm.

Abdomen: Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae moderately elongate (length 2–3 times width); completely sclerotized. Appendix bursae completely sclerotized. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in apical half of corpus bursae; moderately elongate, length between 0.66–1.1 mm; almost vertical.

Larva.—See description, p. 108.

Type material.—*Caradrina triturata* Walker. The lectotype ♂ [BMNH, **here designated**] is labeled: S. Leone, D.F. Morgan, 42-31; Noctuidae genitalia slide No. 3806 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 250. Type locality: Sierra Leone.

Laphygma gratiosa Walker. The holotype (Fig. 252) ♀ [BMNH] is labeled: S. Leone, J. Foxcroft, 53-166; Noctuidae genitalia slide No. 3829 ♀. Type locality: Sierra Leone.

Laphygma bisignata Walker. The lectotype ♂ [BMNH, **here designated**] is labeled: S. Leone, J. Foxcroft, 53-166; Noctuidae genitalia slide No. 3830 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of

species and is illustrated in Fig. 251. Type locality: Sierra Leone.

Material Examined.—Specimens were examined from the following countries: Angola, Democratic Republic of the Congo, Ethiopia, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Malawi, Nigeria, Senegal, Sierra Leone, South Africa, Tanzania, Uganda, Zimbabwe.

Distribution (Fig. 533).—*Spodoptera triturata* is confined to sub-Saharan Africa and the islands of Zanzibar on the east and Principe on the west.

Discussion.—Virtually no variation exists among specimens examined. There is some slight sexual dimorphism with less distinctive forewing marks in the female.

Spodoptera triturata is not known to be a pest of any importance and larval feeding is probably confined to grasses (Brown & Dewhurst 1975).

Spodoptera frugiperda (J.E. Smith)

Figs. 56, 73, 96, 114, 150, 168, 253–258, 305, 323, 353, 385, 417, 449, 489–491, 534

Phalaena frugiperda J.E. Smith 1797: 191, plate 96.
Laphygma macra Guenée *in* Boisduval & Guenée 1852a: 157; Walker 1856: 189; Druce 1889: 267; Viette 1951: 160.
Laphygma inepta Walker 1856: 190.
Prodenia signifera Walker 1856: 193; Druce 1889: 269.
Prodenia plagiata Walker 1856: 194.
Prodenia autumnalis Riley 1871: 109.
Laphygma frugiperda var. *fulvosa* Riley 1876: 49, fig. 27b.
Laphygma frugiperda var. *obscura* Riley 1876: 49, fig. 27c.
Laphygma frugiperda; Walker 1856: 189; Smith 1891: 45; Smith 1893: 168; Grote 1895: 42; Dyar 1902: 123; Hampson 1909: 262; Barnes & McDunnough 1917: 67; Draudt 1926: 256; McDunnough 1938: 96.
Spodoptera frugiperda; Linsley & Usinger 1966: 160; Hayes 1975: 176; Todd & Poole 1980: 726; Franclemont & Todd 1983: 141; Poole 1989: 923; Poole & Gentili 1996: 774.

Diagnosis.—Males resemble *S. ornithogalli*, but apex of forewing of *S. frugiperda* with a distinct white patch and lacking white scales at end of discal cell along veins M and CuA (Figs. 253, 257). Female forewing ground color brown and resembling *S. exigua*, but orbicular spot of *S. frugiperda* is ovate and central scales darker (Figs. 254–256, 258). Male genitalia with valves wide, rectangular, apex truncate; coremata a single lobe, elongate (Figs. 323, 353). Female genitalia ventral plate of ostium bursa elongate, distal margin straight (Fig. 449).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment variably mixed with black and rufous scales, apex cream. Frons with short scales brown; long scales brown; lateral spots at eye margin black; vertex brown. Antenna filiform; scape rufous and cream; flagellum cream (annulated brown becoming brown at mid-length).

Thorax: Patagium light brown with a median brown transverse band. Tegula light brown. Mesothorax light brown. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; first tarsal segment mixed cream and fuscous with cream apical ring, remainder fuscous, second tarsal segment with cream apical ring, lacking apical rings on tarsal segments 3–5. Mesothoracic femur cream and fuscous; tibia fuscous and cream, inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and fuscous; tibia cream and fuscous; first tarsal segment cream mixed with fuscous, segments 2–5 fuscous with cream bases.

Forewing: Length, 10.5–15 mm; ground color brown; basal line absent; short longitudinal black dash at base of Cu vein; R vein from base to reniform spot gray; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line absent; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, cream, with buff to brown center, outlined in black; reniform spot indistinct, partially outlined with black, apex cream with a white V-shaped mark; a small patch of white scales at junction of veins M3 and CuA1 which can extend to orbicular spot; postmedial line black, indistinct, from just below costa to posterior margin, wavy; postmedian band with an indistinct, round, black spot along subterminal line; black scale patches in middle of cells in postmedian area absent; subterminal line white, curved; apex with a white patch; dark gray spindle-

shaped spots along outer margin; fringe gray. Underside ground color pale gray, cream below discal cell, variable amount of cream in discal cell, mixed with cream scales in subterminal area; outer margin with black spots; reniform spot absent.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales (some specimens with outer margin scales extending to anal veins); fringe light brown to pale gray at apex and median line, becoming white toward anal veins. Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray; venter cream and rufous; disto-lateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 323, 353). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate, slightly curved with a decurved apex; extending to just below apex of valve (Figs. 323, 353). Clasper proper absent. Clavus a minute round projection. Sacculus widest at one-third its length, distal half narrow, of constant width; apex truncate. Valvula wider than valve; well differentiated from valve, apex free; apex round; indentation large, ventral margin round. Coremata elongate, more than 0.5 length of valve; composed of a single lobe. Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus membranous. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; short, extending just beyond apex of aedoeagus; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon; a mixture of granular and large spines at apex; dense cornutal patch on apical diverticulum; distal cornutus an ovate plate with large spines at apex.

Adult Female.—Essentially as described for male except:

Thorax: Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment; cream and fuscous, subapical spot absent; first tarsal segment cream with rufous scales, remainder fuscous, apical ring on second tarsal segments only. Mesothoracic femur cream and fuscous; tibia cream and rufous, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and fuscous; tibia cream and fuscous; first tarsal segment cream mixed with fuscous, segments 2–5 fuscous with cream bases.

Forewing: Length, 11–18 mm. Ground color dark brown; basal line absent; R vein not a contrasting color; antemedial line absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, ground colored, outlined in cream; reniform spot absent to being represented by a few cream scales; postmedial line indistinct, beginning below costa and consisting of only a few brown scales that become white below discal cell, wavy; subterminal line absent; apex lacking a white patch; dark gray spindle-shaped spots along outer margin (faint, can be absent); fringe gray. Underside ground color pale gray, cream below discal cell, variable amount of cream in discal cell, mixed with cream scales in subterminal area; outer margin with black spots (faint); reniform spot absent.

Abdomen: Fine dense scales on 8th segment buff.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in basal half of corpus bursae; short, length less than 0.65 mm; forming less than 45 and greater than a 30 degree angle to vertical axis of corpus bursae, oriented left to right.

Larva.—See description, p. 108.

Type material.—*Phalaena frugiperda* J.E. Smith. The type material was not located during this study and is considered lost. The neotype ♂

[USNM, **here designated**] is labeled: MD: Laurel; Prince Georges; Co. Em. 4-X-96; D. C. Ferguson. Reared from; larva on Pokeweed. Photo. USNM ENT 00064639. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 253. Type locality: Laurel, Prince George's County, Maryland, USA.

Laphygma macra Guenée. The lectotype ♀ [MNHP], designated by Viette 1951: 160. Type locality: Colombia.

Laphygma inepta Walker. The lectotype ♀ [BMNH, **here designated**] is labeled: Syntype, Brazil, Santarem, Bates; Noc. gen. Slide No. 3481 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 255. Type locality: Santarem, Brazil.

Prodenia signifera Walker. The lectotype ♂ [BMNH, **here designated**] is labeled: U. S. America, Georgia, 39-6-19, 1522; Noc. gen. Slide No. 3480 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 258. Type locality: Georgia, USA.

Prodenia plagiata Walker. The holotype ♂ (Fig. 257) [BMNH] is labeled: Jamaica, Gosse, 45-110; Noc. gen. Slide No. 3475 ♂. Type locality: Jamaica.

Prodenia autumnalis Riley. The lectotype ♂ [USNM, **here designated**] is labeled: 431, 6/9 84; Type, No. 201, U.S.N.M.; *Laphygma, (Prodenia), autumnalis,* Riley. The lectotype is designated to ensure nomenclatural stability in a common economically important species. Type locality: Missouri. The following syntypes become paralectotypes: (1) ♂, Label data: 5665; Type, No. 201, U.S.N.M.; Collection of, C.V. Riley. (2) ♀, Label data: 431, Nov. 2/ 74; Collection of, C.V. Riley; Type, No. 201, U.S.N.M. (3) ♀, Label data: 381. *Prodenia, autumnalis,* dark caterpillar, Nov. 2/74; Type, No. 201, U.S.N.M.; Collection of, C.V. Riley.

Laphygma frugiperda var. *fulvosa* Riley. The holotype ♂ [USNM] labeled: Tex.; 27/10; Barnes, Collection; 458. var., *fulvosa*; 358 - *Laphygma frugiperda,* var. *fulvosa* Riley - Texas. Type locality: Texas.

Laphygma frugiperda var. *obscura* Riley. The holotype ♀ [USNM] labeled: Tex.; 458. var., *obscura;* 358 - *Laphygma frugiperda,* var. *obscura* Riley - Texas. Type locality: Texas.

Material Examined.—Specimens were examined from the following countries: Antigua, Argentina, Bahamas, Barbados, Belize, Bermuda, Bolivia, Brazil, British Virgin Islands, Canada, Cayman Islands, Chile, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Paraguay, Peru, Puerto Rico, St. Croix, St. Lucia, St. Vincent, Surinam,Trinidad, United States, Uruguay, Venezuela.

Distribution (Fig. 534).—This is a widely distributed species occurring from south central to eastern Canada, coast to coast in the United States, south to Argentina and throughout the Caribbean.

Discussion.—The forewing ground color varies from grayish brown to brown suffused with rufous. The oblique white band between the orbicular and reniform spots can vary in intensity. The white apical patch on the forewing of the male also varies. Sexual dimorphism is present. The forewing maculation in the female is indistinct and the white apical patch is absent.

Spodoptera dolichos (Fabricius)

Figs. 79, 92, 134, 145, 160, 259, 324, 354, 386, 418, 450, 492–494, 535

Noctua dolichos Fabricius 1794: 95.

Phalaena commelinae J.E. Smith 1797: 189, plate 95.

Trigonophora commelinae; Hübner 1816: 217.

Phalaena marmorea Sepp [1840]: 109, plate 51; [synonymized by Poole 1989: 924].

Prodenia commelinae; Guenée *in* Boisduval & Guenée 1852a: 162; Walker 1856: 192; Druce 1889: 268; Smith 1891: 45; Smith 1893: 169; Grote 1895: 42; Dyar 1903 : 123.

Prodenia dolichos; Hampson 1909: 242; Barnes & McDunnough 1917: 67; Draudt 1924: 255; McDunnough 1938: 96; Richards 1941: 239; Linsley & Usinger 1966: 160.

Spodoptera dolichos; Hayes 1975: 176; Franclemont & Todd 1983: 141; Poole 1989: 923; Poole & Gentili 1996: 774.

Diagnosis.—Easily distinguished from *S. androgea* by dark brown and black stripe on inner margin of tegulae of *S. dolichos* (Fig. 259). Forewing with medial curved white band not extending to tornus. Male genitalia with ampulla narrower than *S. androgea* and apex of sacculus distinct from valve (compare Figs. 354 and 355). Female genitalia with signum longer than *S. androgea* and almost vertical (compare Figs. 418 and

419). Striations of corpus bursae tightly convoluted (Fig. 418).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment variably mixed with black and rufous scales, apex cream. Frons with short scales rufous and cream; long scales rufous and cream; lateral spots at eye margin absent; vertex cream to pale rufous. Antenna filiform; scape rufous (mixed with a few black scales anteriorly); flagellum rufous (annulated with black becoming brown at mid-length).

Thorax: Patagium banded, basal band light brown to brown mixed with black scales, a thin black band separates basal band from a median white band, distal band light brown to brown with a few to a patch of black scales, medial apex white. Tegula with lateral two-thirds light brown, thin black stripe separating median brown quarter. Mesothorax light brown. Underside of thorax white. Prothoracic femur rufous and fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; tarsal segments cream, mixed with rufous laterally. Mesothoracic femur cream and rufous; tibia cream and rufous, inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments rufous, fuscous at base with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments rufous, fuscous at base with cream apical rings.

Forewing: Length, 18–21 mm; ground color brown; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal triangular scale patch between R and Cu veins gray bordered by cream (can be mixed with rosy scales); basal half circle scale patch below Cu vein brown bordered by black; antemedial line dark reddish brown, indistinct; claviform spot absent; basal scale patch small, gray, from midway between M and anal veins to anal vein; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique trapezoid, cream, with a light brown center bordered by black; reniform spot brown with an elongate cream center, proximal border cream, distal border black; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 and down vein CuA2 to postmedial line; postmedial line indistinct, gray; postmedian band with an elliptical brown spot along subterminal line; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area; subterminal line white, curved; apex with a white patch; black triangular-shaped spots along outer margin; fringe brown. Underside ground color pale gray; outer margin with black spots; reniform spot gray.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales; fringe cream at apex becoming white at vein CuA1. Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray; venter cream and rufous; disto-lateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa with base straight, broadly curved distally (Figs. 324, 354). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex round; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a decurved apex; extends to just below apex of valve (Figs. 324, 354). Clasper proper absent. Clavus elongate, finger-shaped. Sacculus broad to three-fourths its length, abruptly narrowing to an elongate projection distally; apex pointed. Valvula wider than valve; well differentiated from valve, apex free; apex round; indentation of ventral margin forming a small pocket. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus with minute granules. Vinculum a broad U-shape with bowed arms and a robust base. Aedoeagus sinuous; coe-

cum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch quadrate; length moderate, extending to before middle of vesica; cornuti a mixture of small and large spines; lateral cornutal patch absent; dense cornutal patch at apex of vesica; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Forewing: Length, 20–22 mm.

Abdomen: Fine dense scales on 8th segment gray.

Genitalia: Ventral plate of ostium bursa wider than high; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae elongate, length greater than twice width; striate convolutions. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; almost vertical.

Larva.—See description, p. 109.

Type material.— *Noctua dolichos* Fabricius. The type is presumed lost (Zimsen 1964). The neotype ♂ [USNM, **here designated**] is labeled: Florida:; N. Key Largo; 28 Nov. 1976; D. C. Ferguson. USNM ENT 00062017. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 259. Type locality: U.S.A., Florida, N. Key Largo.

Phalaena commelinae J.E. Smith. The type repository is unknown. Type locality: Georgia, USA.

Phalaena marmorea Sepp. The type repository is unknown. Type locality: Surinam.

Material Examined.—Specimens were examined from the following countries: Bahamas, Brazil, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, El Salvador, Grenada, Guadeloupe, Guatemala, Guyana, Honduras, Jamaica, Mexico, Nicaragua, Panama, Paraguay, Peru, Puerto Rico, St. Lucia, St. Vincent, Tobago, Trinidad, United States, Venezuela, Virgin Islands.

Distribution (Fig. 535).—This species is distributed in the eastern United States from New York south to Florida and west to southern Texas. In the Neotropics it ranges from Mexico through Central America to South America as far south as Paraguay and southern Brazil. In the Caribbean it has been found from Cuba and Jamaica east to Dominican Republic and Puerto Rico south along the Lesser Antilles to Trinidad and Tobago.

Discussion.—There appears to be little variation within *S. dolichos,* other than intensity of the forewing ground color and the amount of brown scales associated with the leading edge of the hindwing. Sexual dimorphism is absent.

Spodoptera androgea (Stoll)

Figs. 54, 65, 72, 91, 108, 149, 260–262, 325, 355, 387, 419, 451, 495–497, 536

Phalaena Noctua androgea Stoll *in* Cramer 1782: 42, plate 310, fig. D (1780); index p. 247 (1782). This combination occurs only in the index, therefore the name dates from 1782 (Poole 1989).

Prodenia rubrifusa Hampson 1909: 240; Draudt 1926: 255.

Prodenia androgea; Walker 1856: 195; Druce 1889: 269; Draudt 1926: 255.

Spodoptera androgea; Todd & Poole 1980: 730; Poole 1989: 922.

Diagnosis.— Most similar to *S. dolichos,* but *S. androgea* lacks dark vertical stripes on inner margin of tegulae. Forewing with a distinct, curved white band from basal third of costa to tornus (Figs. 260–262). Male genitalia with ampulla wider than in *S. dolichos* (compare Figs. 354 and 355), sacculus of *S. androgea* not as well differentiated at apex (Fig. 355). Female genitalia with signum shorter than *S. dolichos* and oriented at less than a 45° angle to vertical axis of corpus bursae; striations of corpus bursae straight, not tightly convoluted as in *S. dolichos* (compare Figs. 418 and 419).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment variably mixed with black and rufous scales, apex cream. Frons with short scales cream to rufous; long scales brown to rufous; lateral spots at eye margin absent; vertex cream and brown (can be mixed with rufous scales). Antenna filiform; scape cream to rufous; flagellum cream.

Thorax: Patagium pale rufous to light brown or

brown with thin black basal band and median white transverse band. Tegula pale rufous to light brown. Mesothorax pale rufous to light brown and white. Underside of thorax pale rufous to cream. Prothoracic femur fuscous and cream (can be mixed with rufous scales); tibia with lateral scale tufts not extending beyond first tarsal segment, rufous, black, and cream, subapical spot absent; tarsal segments cream. Mesothoracic femur cream and rufous; tibia cream and rufous, inner spur less than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments rufous, fuscous at base with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments rufous, fuscous at base with cream apical rings.

Forewing: Length, 18–20 mm; ground color brown; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal elliptical scale patch between R and Cu veins centered with black (can have some gray scales); basal half circle scale patch below Cu vein brown bordered by black; antemedial line black, indistinct; claviform spot absent; basal scale patch gray mixed with black scales from R vein to posterior margin and proximal to antemedial line; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique trapezoid, cream, with a light brown center bordered by light brown to black; reniform spot indistinct, black and brown with a cream dash at distal apex; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 and down vein CuA2 to postmedial line; postmedial line black, indistinct, from just below costa to posterior margin, wavy; postmedian band divided, pale gray anterior and brown and black posterior patches and with an elliptical brown spot along subterminal line; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area; subterminal line white, curved; apex with a white patch; black spindle-shaped spots along outer margin; fringe brown. Underside ground color pale gray; outer margin with black spots; reniform spot large dark gray patch between veins Sc and R and covering discal cell.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales; fringe rufous at apex becoming white toward anal veins. Underside ground color white; costal cells C and Sc white speckled with brown and rufous scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray to cream; venter cream and rufous; disto-lateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa with base straight, broadly curved distally (Figs. 325, 355). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, slightly curved with a decurved apex; extends to just below apex of valve (Figs. 325, 355). Clasper proper absent. Clavus elongate, finger-shaped. Sacculus broad to two-thirds its length, tapering distally; apex pointed. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation ventral margin forming a small pocket. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus with minute granules. Vinculum a broad U-shape with bowed arms and a robust base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch a wide ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute granules to an area of larger connate spines at apex; lateral cornutal patch covering median diverticulum; a mixture of elongate spines at median diverticulum becoming finer over remaining area; dense cornutal patch subapical on vesica; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Forewing: Length, 19–22 mm.

Abdomen: Fine dense scales on 8th segment gray.

Genitalia: Ventral plate of ostium bursa wider than high; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae moderately elongate (length 2–3 times width); a distinct sclerotized mid-ventral band. Appendix bursae completely sclerotized. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in apical half of corpus bursae; moderately elongate, length between 0.66–1.1 mm; forming less than a 30 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 110.

Type material.—*Phalaena Noctua androgea* Stoll. The type material was not located during this study and is considered lost. The neotype ♂ [USNM, **here designated**] is labeled: Dominica; Grand Savane; VI-14-1964; O. S. Flint, Jr. USNM ENT 00061442. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 260. Type locality: Grand Savane, Dominica.

Prodenia rubrifusa Hampson. The holotype ♂ (Fig. 262) [BMNH] is labeled: Holotype, Runaway Bay, Jamaica, 31. 3. 1905, Wlsm. Type locality: Runaway Bay, Jamaica.

Material Examined.—Specimens were examined from the following countries: Bolivia, Brazil, Colombia, Costa Rica, Cuba, Dominica, Ecuador, French Guiana, Grenada, Guatemala, Jamaica, Panama, Peru, Puerto Rico, St. Lucia, St. Vincent, United States, Venezuela.

Distribution (Fig. 536).—This species is distributed from southern Florida, throughout the Antilles, Guatemala, Costa Rica, Panama, south to Venezuela, Brazil, and Peru. Specimens from Florida were first collected from Fuchs Hammock, Homestead, Dade Co., on 27 November 1984. Other specimens are from No Name Key, Monroe Co., 19 March 1987; Charles Deering Estate (Miami), Dade Co., 25 April 1989; and Big Cypress National Preserve, Collier Co., 7 April 1989 (Dickel 1991). It may be that *S. androgea* has become established in southern Florida, but more records are needed to confirm this.

Discussion.—There is a distinct reddish color form of *S. androgea* that Hampson (1909) described as *S. rubrifusa*. This reddish form occurs in Jamaica and Puerto Rico, with a single specimen examined from Dominica. The other specimens from Dominica are all typical *S. androgea*. The other islands in the Antilles from which specimens are available are all typical *S. androgea*, and include Cuba, Grenada, St. Lucia, and St. Vincent. There appears to be little other variation either in the reddish form or in typical *S. androgea*. Sexual dimorphism is present in typical *S. androgea*, with the male having an ochreous median area of the forewing between the antemedial and postmedial lines below vein M. There appears to be no sexual dimorphism in the reddish form.

Spodoptera littoralis (Boisduval)

Figs. 163, 263–267, 326, 356, 388, 420, 452, 498–500, 537

Hadena littoralis Boisduval 1833: 91.

Hadena retina Freyer 1845: 161, plate 478, figs. 2,3; Walker 1856: 192.

Prodenia testaceoides Guenée *in* Boisduval & Guenée 1852a: 165, plate 6, fig. 7; Viette 1951: 160; Walker 1856: 195.

Prodenia littoralis; Mabille 1879: 320; Cotes & Swinhoe 1888: 325 ; Swinhoe 1890: 227; Hampson 1894: 247.

Spodoptera littoralis; Viette 1963: 147; Brown & Dewhurst 1975: 256; Goater 1983: 277; Poole 1989: 924.

Diagnosis.—Color and pattern almost indistinguishable from *S. litura*. Hindwing with apices of veins white. Male genitalia with juxta quadrate; ampulla more robust than in *S. litura* (compare Figs. 356 and 357); dorsal lobes of coremata much shorter than ventral lobes (Fig. 356). Female genitalia with distal margin of ventral plate of ostium bursa straight (Fig. 452); ductus bursae shorter than *S. litura* (compare Figs. 420 and 421).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment black, apex cream. Frons with short scales cream; long scales brown and cream; lateral spots at eye margin brown to black; vertex cream and brown. Antenna filiform; scape cream to light brown; flagellum cream.

Thorax: Patagium light brown to brown flecked with black, median transverse band white, apical margin white. Tegula light brown and white (black scales at caudomedial apex). Mesothorax with light brown and brown scales,

some tipped white. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot black; tarsal segments cream. Mesothoracic femur fuscous and cream; tibia fuscous and cream, inner spur less than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments 1–4 fuscous with cream apical rings, segment 5 cream. Metathoracic femur cream and fuscous; tibia cream, rufous, and fuscous; tarsal segments 1–4 cream with bases fuscous, segment 5 cream.

Forewing: Length, 12–16 mm; ground color brown; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal triangular scale patch between R and Cu veins brown bordered by white; basal half circle scale patch below Cu vein light brown bordered by black; antemedial line black, indistinct; claviform spot absent; basal scale patch small, gray, from midway between M and anal veins to anal vein; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique trapezoid, cream, with a light brown center bordered by light brown to black; reniform spot brown outlined in white on proximal border, distal apex is a triangular light brown spot outlined in white, a white distal border extending to middle; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line indistinct, black variably bordered by white from middle to posterior margin; postmedian band pale gray and with an elliptical brown spot along subterminal line; black scale patches in middle of cells M2 to CuA1 in postmedian area; subterminal line a light brown band bordered by white; apex with a few white scales, no distinct patch; dark gray spindle-shaped spots along outer margin; fringe gray. Underside ground color pale gray; outer margin with black crescent-shaped spots; reniform spot gray.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales; fringe white. Underside ground color white; costal cells C and Sc cream speckled with pale gray scales; outer margin with a few faint gray spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray; venter cream to pale gray; disto-lateral black spots on sternites (can be indistinct to absent); 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus evenly curved; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa straight (Figs. 326, 356). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate, slightly curved with a decurved apex; extends beyond apex of valve (Figs. 326, 356). Clasper proper absent. Clavus a minute round projection. Sacculus widest at one-fourth its length, tapering distally; apex pointed. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation large, ventral margin round. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a broad rectangular band with ventrolateral projections, median process not constricted, ventral margin concave. Anellus membranous. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a wide ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch an elongate elliptical area; a mixture of small spines distally and large spines apically; dense cornutal patch subapical on vesica; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Forewing: Length, 13–16 mm. Longitudinal black dash at base absent; R vein not a contrasting color; gray patch covering anal cell and half of cell CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique trapezoid, cream, with a gray center, bordered by thin black line distally; reniform spot more gray with a light brown to gray apical spot outlined in white; postmedian band less distinct and tends to be more brown; black scale patches

in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area.

Abdomen: Fine dense scales on 8th segment cream.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin straight; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae membranous. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in apical half of corpus bursae; short, length less than 0.65 mm; forming greater than a 45 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 110.

Type material.—*Hadena littoralis* Boisduval. The type material was not located during this study and is considered lost. The neotype ♂ [USNM, **here designated**] is labeled: Uganda; Ankole; Kichwamba; IV-23-29-68; P. J. Spangler. Genitalia Slide; By MGP ♂; USNM 46193. SPOD 0216. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 263. Type locality: Kichwamba, Ankole, Uganda.

Hadena retina Freyer. The type repository is unknown. Type locality: Crete, Greece.

Prodenia testaceoides Guenée. The lectotype ♂ is deposited in the MNHP, designated by Viette 1951: 160. Type locality: Mauritius.

Material Examined.—Specimens were examined from the following countries: Algeria, Angola, British Indian Ocean Territory, Cameroon, Canary Islands, Comoro Islands, Democratic Republic of the Congo, Egypt, Equatorial Guinea, Ethiopia, Gambia, Ghana, Guinea Republic, Ile Maurice, Israel, Ivory Coast, Kenya, Liberia, Madagascar, Malawi, Mauritius, Namibia, Niger, Nigeria, Pakistan, Principe Island, Réunion, São Tomé Island, Senegal, Seychelles, Sierra Leone, South Africa, St. Helena, Tanzania, Uganda, Zimbabwe.

Distribution (Fig. 537).—This species ranges from southern Europe and Africa east to the Middle East and western Asia including the Arabian Peninsula, Iran, Iraq, and Pakistan. It is also found in the Seychelles, Mauritius, Réunion, and Rodrigues in the Indian Ocean (Brown & Dewhurst 1975).

Discussion.—Typical variation is found in the intensity of the forewing ground color. Sexual dimorphism is present with the ochreous median area of the forewing between the antemedial and postmedial lines and below vein M in the male. The orbicular spot is larger and more intense in the male.

Aurivillius (1897) synonymized *S. littoralis* under *S. litura.* Viette (1963) resurrected *S. littoralis* based on characters of the male and female genitalia. Care should be taken when referring to these species in the older economic literature and distribution should dictate what species is actually being discussed. *Spodoptera littoralis* is essentially western Palaearctic to Pakistan and Afrotropical, whereas *S. litura* is Oriental, Australasian, and Oceania in distribution.

Spodoptera litura (Fabricius)

Figs. 74, 87, 100, 129, 143, 158–159, 268–277, 327, 357, 389, 421, 453, 501–503, 537

Noctua litura Fabricius 1775: 601; Aurivillius 1897: 162.
Noctua histrionica Fabricius 1775: 612.
Noctua elata Fabricius 1781: 220.
Prodenia tasmanica Guenée *in* Boisduval & Guenée 1852a: 163; Walker 1856: 198.
Prodenia ciligera Guenée *in* Boisduval & Guenée 1852a: 164; Walker 1856: 196.
Prodenia subterminalis Walker 1856: 196.
Prodenia glaucistriga Walker 1856: 197
Prodenia declinata Walker 1857b: 723.
Mamestra albisparsa Walker 1862: 186.
Prodenia evanescens Butler 1884: 94.
Prodenia litura; Chen *et al.* 1991: 230; Warren *in* Seitz 1914b: 320.
Spodoptera litura; Viette 1963: 147; Holloway 1976: 12; Barlow 1982: 86; Sugi 1982: 764; Goater 1983: 278; Holloway 1989: 136; Poole 1989: 924; Edwards 1996: 324; Kononenko *et al.* 1998: 233.

Diagnosis.—Color and pattern almost indistinguishable from *S. littoralis.* Hindwing of *S. litura* with apices of veins brown. Male genitalia with juxta triangulate; base of ampulla narrower, than in *S. littoralis* (compare Figs. 356 and 357); dorsal lobes of coremata almost as long as ventral lobes (Fig. 357). Female genitalia with distal margin of ventral plate of ostium bursa a broad V-shaped notch (Fig. 453); ductus bursae longer than *S. littoralis* (compare Figs. 420 and 421).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band

variably mixed with rufous scales; apical segment black, apex cream. Frons with short scales cream; long scales brown and cream; lateral spots at eye margin brown to black; vertex cream and brown. Antenna filiform; scape cream and brown; flagellum cream and brown.

Thorax: Patagium light brown to brown flecked with black, median transverse band white, apical margin white. Tegula light brown and white (black scales at caudomedial apex). Mesothorax light brown. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream (can have fuscous scales present), subapical spot black; tarsal segments cream. Mesothoracic femur cream (mediolateral subapical patch fuscous); tibia fuscous and cream, inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments 1–4 fuscous with cream apical rings, segment 5 cream. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments 1–4 cream with bases fuscous, segment 5 cream.

Forewing: Length, 14–17 mm; ground color brown; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal triangular scale patch between R and Cu veins brown bordered by white; basal half circle scale patch below Cu vein light brown bordered by black; antemedial line black, indistinct; claviform spot absent; basal scale patch gray from costa to posterior margin (indistinct above Cu vein); gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique trapezoid, cream, with a light brown center bordered by light brown to black; reniform spot brown outlined in white on proximal border, distal apex is a triangular light brown spot outlined in white, a white distal border extending to middle; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line indistinct, black variably bordered by white from middle to posterior margin; postmedian band pale gray and with an elliptical brown spot along subterminal line; black scale patches in middle of cells M2 to CuA1 in postmedian area; subterminal line a light brown band bordered by white; apex with a few white scales, no distinct patch; dark gray spindle-shaped spots along outer margin; fringe gray. Underside ground color pale gray; outer margin with black crescent-shaped spots; reniform spot gray.

Hindwing: Ground color white; apex, outer margin, and veins with light brown scales; fringe white. Underside ground color white; costal cells C and Sc cream speckled with rufous and gray scales; outer margin with a few faint gray spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray to gray; venter cream (rufous scales can be present); disto-lateral black spots on sternites absent (can have a few remnant scales on some specimens); 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 327, 357). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate, slightly curved with a decurved apex; extending to just below apex of valve (Figs. 327, 357). Clasper proper absent. Clavus a minute round projection. Sacculus widest at one-fourth its length, tapering distally; apex truncate. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation large, ventral margin round. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process narrow at base and elongate, ventral margin narrowly concave. Anellus membranous. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a wide ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch an elongate elliptical area; a mixture of small spines distally and large spines apically; dense cornutal patch subapical on vesica; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Forewing: Length, 15–18 mm. Longitudinal black dash at base absent; basal scale patch small, gray, from midway between M and anal veins to anal vein; gray patch covering anal cell and half of cell CuA2 absent; orbicular spot an oblique trapezoid, cream, with a gray center, bordered by thin black line distally; reniform spot more gray with a light brown to gray apical spot outlined in white; postmedian band less distinct and tends to be more brown; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area.

Abdomen: Fine dense scales on 8th segment cream.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin with a broad V-shaped notch; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae elongate (length greater than 3 times width); completely sclerotized. Appendix bursae membranous. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in apical half of corpus bursae; short, length less than 0.65 mm; almost vertical.

Larva.—See description, p. 111.

Type material.—*Noctua litura* Fabricius. The type is presumed lost (Zimsen 1964). The neotype ♂ [USNM, **here designated**] is labeled: Indien WB 1800m; Darjeeling Mangpu-road; 11-VII-1986; leg. W. Thomas. SPOD 0360. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 269. Type locality: Darjeeling Mangpu road, India.

Noctua histrionica Fabricius. The type is presumed lost (Zimsen 1964). Type locality: India.

Noctua elata Fabricius. The type is presumed lost (Zimsen 1964). Type locality: Tranquebariae, India.

Prodenia tasmanica Guenée. The type repository is unknown. Type locality: Tasmania, Australia.

Prodenia ciligera Guenée. The lectotype ♂ [BMNH, **here designated**] is labeled: [No locality label] 60.15, EIC; *Prod. ciligera;* Noc. gen. Slide No. 3497 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 274. Type locality: Java, Indonesia. The following syntype becomes a paralectotype: Label data: 60.15, EIC; *Prod. ciligera.*

Prodenia subterminalis Walker. The lectotype ♀ [BMNH] is labeled: Lectotype, Punjab, Hearsay, 54-74; Noc. gen. Slide No. 3498 ♀. Walker (1856: 196) described *subterminalis* from two specimens of unknown sex, one from Punjab, and the other from North[ern] India. Hampson (1909: 247) listed "1 ♀ type *subterminlais*" from his list of specimens from Punjab. This can be inferred as a lectotype designation and this specimen is the one mentioned above and is illustrated in Fig. 277.

Prodenia glaucistriga Walker. The lectotype ♂ [BMNH, **here designated**] is labeled: N. India, Noc. gen. Slide No. 3486 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 276. Type locality: N. India. The following syntype becomes a paralectotype: ♂, Label data: Canara, S. N. Ward, 50-26.

Prodenia declinata Walker. The holotype ♂ (Fig. 273) [BMNH] is labeled: Holotype, N. India, 43-10; Noc. gen. Slide No. 3499 ♂. Type locality: N. India.

Mamestra albisparsa Walker. The type(s) are deposited in University Museum, Oxford University, Oxford. Type locality: Borneo, Sarawak, Indonesia.

Prodenia evanescens Butler. The lectotype ♀ [BMNH, **here designated**] is labeled: S. Pacific, Caroline Is., E. G. Holden, 84-2; *Prodenia, evanescens,* type Butler; Noc. gen. Slide No. 3500 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 275. Type locality: Caroline Is., Federated States of Micronesia. The following syntype becomes a paralectotype: Label data: S. Pacific, Caroline Is., E. G. Holden, 84-2; Caroline Isl., 84-2.

Material Examined.—Specimens were examined from the following countries: American Samoa, Australia, Burma, China, Chirstmas Island, Cook Islands, Federated States of Micronesia, Fiji, French Polynesia, Guam, Hong Kong, India, Indonesia, Japan, Kiribati, Line Islands, Malaysia, Maldive Islands, Marshall Islands, Nepal, New Caledonia, New Zealand, Northern Marianas, Palau, Papua New Guinea, Philippines, Pitcairn Island, Singapore, Sri Lanka, Taiwan, Thailand, Tonga, United States (Hawaii), Vanuatu, Western Samoa.

Distribution (Fig. 537).—*Spodoptera litura* is distributed further east than *S. littoralis.* Care must be taken when examining specimens from western Asia as *S. litura* reaches Afghanistan, northwestern India, and Pakistan. From western

Asia, *S. litura* ranges eastward to Korea, China, and Japan, southward throughout the Australasian area, and is widely distributed across the Pacific to Hawaii.

Discussion.—Variation exists in the forewing ground color ranging from brown to cream. The lighter colored specimens are dominant among the islands of the Western Pacific. The ground color exhibits its full range in the Marquesas Islands. Lighter forms are found on Kiribati, Christmas Island, Henderson Island, Marshall Islands, and the Northern Marianas. The darker form is found in the Oriental and Australasian realms, including the Philippines and Indonesia.

Sexual dimorphism is present. The male has an ochreous forewing patch between the antemedial and postmedial lines below vein M. Not all specimens show sexual dimorphism; some males have no ochreous patch. The orbicular spot is more solid in the male.

Spodoptera picta (Guérin-Méneville)

Figs. 43, 48, 117, 278, 328, 358, 390, 422, 454, 504–506, 538

Phalaena festiva Donovan 1805: pl. 36, fig. 1 [Preoccupied, junior primary homonym of *Phalaena festiva* Cramer 1775.

Polia picta Guérin-Méneville *in* Duperrey 1831: pl. 19, fig. 7; 1838: 285.

Calogramma festiva; Walker 1856: 198; Hampson 1909: 239; Warren *in* Seitz 1914b: 319.

Spodoptera picta; Sugi 1982: 763; Holloway 1979: 416; Holloway 1989: 138; Poole 1989: 925; Edwards 1996: 324.

Diagnosis.—Similar to no other species of *Spodoptera.* Forewing ground color cream; irregular patch of rose scales from oblique ground color band to postmedian line between costa and R vein (Fig. 278). Hindwing completely white. Male genitalia similar to *S. littoralis,* but coremata shorter in *S. picta* (compare Figs. 326 and 328). Female genitalia similar to *S. litura,* but V-shaped notch on distal margin of ventral plate of ostium bursa shallower in *S. picta* (compare Figs. 453 and 454).

Description. Adult Male.—*Head:* Basal segment of labial palpus rufous surrounded by cream scales; median segment mixed with black and brown scales in basal half, cream apically to cream variably mixed with rufous and black scales; apical segment cream mixed with rufous scales. Frons with short scales cream; long scales reddish orange and cream; lateral spots at eye margin absent; vertex cream and reddish orange. Antenna filiform; scape cream; flagellum cream.

Thorax: Patagium cream with basal and subapical band orange. Tegula orange and cream. Mesothorax orange anteriorly, cream posteriorly. Underside of thorax white. Prothoracic femur rufous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; tarsal segments cream. Mesothoracic femur cream; tibia cream and rufous, inner spur less than twice length of outer spur, spurs completely scaled; tarsal segments cream, rufous at base of segment 1. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments cream.

Forewing: Length, 18–19 mm; ground color cream; basal line absent; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein cream broadly bordered by black; antemedial line black and white, indistinct; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique ground color band extending from costa to below Cu vein with a thin oblique black line between veins R and Cu; reniform spot an irregular patch of rose scales from oblique ground color band to postmedian line between costa and R vein, between R and CuA1 veins scattered patches of black scales, irregular patches of rose scales between veins CuA2 and posterior margin; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line irregular with black patches at costa to middle then becoming rose to posterior margin; postmedian band undifferentiated; black scale patches in middle of cells M2 to CuA2 in postmedian area; subterminal line absent; apex lacking a white patch; spots along outer margin absent; fringe cream. Underside ground color cream with scattered pale gray patches; outer margin spots absent; reniform spot patch of rose scales corresponding to similar patch on upper side of forewing.

Hindwing: Ground color white; immaculate; fringe white. Underside ground color white; costal cells C and Sc cream speckled with rufous scales (can be mixed with a few gray scales); outer margin spots absent; no spot on underside.

Abdomen: Dorsum cream; venter cream (rufous

scales can be present); disto-lateral dark rufous spots on sternites; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 328, 358). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate, slightly curved with a decurved apex; extending to just below apex of valve (Figs. 328, 358). Clasper proper absent. Clavus a minute round projection. Sacculus widest at one-fourth its length, tapering distally; apex truncate. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation large, ventral margin round. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process narrow at base and elongate, ventral margin narrowly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch a wide ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch an elongate elliptical area; a mixture of small spines distally and large spines apically; dense cornutal patch subapical on vesica; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Forewing: Length, 20.5–22 mm.

Abdomen: Fine dense scales on 8th segment cream.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin with a broad V-shaped notch; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum at middle of corpus bursae; short, length less than 0.65 mm; almost vertical.

Larva.—See description, p. 112.

Type material.—*Polia picta* Guérin-Méneville. The type material was not located during this study and is considered lost. The neotype ♂ [USNM, **here designated**] is labeled: Australia: Qld.; Kuranda;14 April 1980; G. F. Hevel & J. A. Fortin. SPOD 1402. The neotype is designated and labeled to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 278. Type locality: Kuranda, Queensland, Australia.

Phalaena festiva Donovan.The type repository is unknown. Type locality: New South Wales, Australia.

Material Examined.—Specimens were examined from the following countries: American Samoa, Australia, Burma, China, Christmas Island, Fiji, India, Indonesia, Key Island, Malaysia, Maldive Islands, New Caledonia, Papua New Guinea, Philippines, Singapore, Solomon Islands, Sri Lanka, Taiwan, Vanuatu, Vulcan Islands, Western Samoa.

Distribution (Fig. 538).—*S. picta* is distributed from India east to China, Taiwan, and Japan, and south to the Philippines, Papua New Guinea, and Australia.

Discussion.—This is the most easily recognized species of *Spodoptera.* The forewing pattern has the same elements as in *S. littoralis* and *S. litura,* only the colors are different. There is no sexual dimorphism.

Spodoptera evanida Schaus

Figs. 33, 279–281, 329, 359, 391, 423, 455, 539

Spodoptera evanida Schaus 1914: 490; Draudt 1926: 256; Todd & Poole 1980: 728; Poole 1989: 923; Poole & Gentili 1996: 774.

Diagnosis.—Forewing ground color rufous, orbicular spot oval, overall pattern indistinct. Hindwing mostly pure white with a small patch of rufous scales at apex, a few rufous scales along outer margin and at ends of veins. Male genitalia with a broad ampulla and a large costal process that is curved parallel to costa (Fig. 359). Female genitalia with distal margin of ventral plate of ostium bursa U-shaped (Fig. 455).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; me-

dian segment cream variably mixed with rufous and black scales and mixed with black and brown scales in basal half, cream apically; apical segment cream. Frons with short scales cream; long scales cream; lateral spots at eye margin absent; vertex cream. Antenna filiform; scape cream; flagellum cream.

Thorax: Patagium cinnamon. Tegula rufous. Mesothorax cinnamon. Underside of thorax cream. Prothoracic femur cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream, subapical spot absent; tarsal segments cream. Mesothoracic femur cream; tibia cream, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments light brown with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments cream.

Forewing: Length, 13–16 mm; ground color rufous; basal line absent; longitudinal black dash at base absent; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line absent; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, pale rufous; reniform spot absent; no white scales along Cu vein and bases of M3 and CuA1 veins; postmedial line indistinct, gray; postmedian band undifferentiated; black scale patches in middle of cells in postmedian area absent; subterminal line reddish brown, indistinct; apex lacking a white patch; spots along outer margin absent; fringe rufous. Underside ground color rufous; outer margin spots absent; reniform spot absent.

Hindwing: Ground color white; a small patch of rufous scales at apex, a few rufous scales along outer margin and at ends of veins; fringe white. Underside ground color white; costal cells C and Sc cream speckled with rufous scales; outer margin spots absent; no spot on underside.

Abdomen: Dorsum cream; venter cream and rufous; disto-lateral black spots on sternites absent; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa convex (Figs. 329, 359). Costal process elongate, wide, heavily sclerotized; at base of costa on inner edge; parallel to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, broad, curved with a decurved apex; extending to just below apex of valve (Figs. 329, 359). Clasper proper absent. Clavus large, club-shaped, base narrower than apex. Sacculus fairly constant throughout length, slightly constricted at two-thirds its length; apex rounded dorsally, truncate ventrally. Valvula wider than valve; well differentiated from valve, apex free; apex round; indentation narrow, deep, ventral margin slightly curved. Coremata moderately elongate, approximately 0.5 or less length of valve; composed of a single lobe. Juxta a narrow rectangular band, median process narrow at base and elongate, ventral margin narrowly concave. Anellus with minute granules. Vinculum a broad U-shape with bowed arms and a robust base. Aedoeagus straight; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; short, extending just beyond apex of aedoeagus; cornuti in form of minute flat granules; lateral cornutal patch a wide elongate ribbon; a mixture of granular and large spines at apex; dense cornutal patch on apical diverticulum; distal cornutus an indistinct flat plate.

Adult Female.—Essentially as described for male except:

Forewing: Length, 15 mm.

Abdomen: Fine dense scales on 8th segment buff.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin U-shaped; ventrolateral invaginated pocket of 8th sternite large, well developed laterally. Ductus bursae elongate (length greater than 3 times width); partially sclerotized. Appendix bursae completely sclerotized. Corpus bursae bulbous, length less than twice width; smooth. Signum in apical half of corpus bursae; short, length less than 0.65 mm; almost vertical.

Larva.—Unknown.

Type material.—*Spodoptera evanida* Schaus. The holotype ♂ [USNM] is labeled: Cayenne, F. Guiana; Collection, Wm Schaus; Type, No. 16534 [red Label]; *Spodoptera, evanida,* type Schs [hand written]. Type locality: Cayenne, French Guiana.

Material Examined.—Specimens were exam-

ined from the following countries: Brazil, Colombia, French Guiana, Venezuela.

Distribution (Fig. 539).—*S. evanida* has a restricted distribution from Colombia, Venezuela, French Guiana, south through Amazonian Brazil to Espirito Santos.

Discussion.—There is little variation in the forewing ground color. No sexual dimorphism is present. *Spodoptera evanida* with its rufous forewing, indistinct maculation, and pure white hindwing is unlikely to be confused with any other species of *Spodoptera.*

Spodoptera latifascia (Walker)

Figs. 44, 66, 80, 108, 142, 161–162, 282–284, 330, 360, 392, 424, 456, 507–509, 539

Prodenia latifascia Walker 1856: 195; Barnes & McDunnough 1917: 67; Draudt 1926: 255; McDunnough 1938: 96.

Prodenia variolosa Walker 1857b: 722; Druce 1889: 269.

Spodoptera latifascia; Hayes 1975: 174; Levy & Habeck 1976: 586; Todd & Poole 1980: 730; Franclemont & Todd 1983: 141; Poole 1989: 924; Poole & Gentili 1996: 774.

Diagnosis.—Similar to *S. descoinsi* and *S. cosmiodes*. Forewing of male with orbicular spot wider than *S. descoinsi* and white field not as distinct. Can easily be confused with *S. ornithogalli,* spots of adterminal line are spindle-shaped in *S. latifascia* and crescent-shaped in *S. ornithogalli.* Length to width ratio of forewing greater than 2.5, in *S. ornithogalli* ratio is less than 2.5. Hindwing margin outlined with more light brown scales than in *S. descoinsi* or *S. cosmiodes*; in *S. ornithogalli* veins covered with light brown scales. Male genitalia with ampulla narrower and apex less produced than in *S. descoinsi* (compare Figs. 360 and 362), juxta more robust (compare Figs. 330 and 332). Female genitalia with distal margin of ventral plate of ostium bursa a wide U-shaped groove (Fig. 456); signum longer than in *S. descoinsi* (compare Figs. 424 and 426), fine dense scales on 8th segment black.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment variably mixed with black and rufous scales, apex cream. Frons with short scales cream; long scales cream; lateral spots at eye margin rufous to brown (can form into a bar); vertex cream. Antenna filiform; scape cream to rufous; flagellum cream.

Thorax: Patagium light brown mixed with brown scales, some tipped white, transverse rows of black scales. Tegula light brown and brown. Mesothorax light brown and brown scales, some tipped white. Underside of thorax white. Prothoracic femur rufous and fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot black; tarsal segments fuscous, proximal and apical rings cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur cream; tibia cream, inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments cream with pale fuscous bases. Metathoracic femur cream; tibia cream (can have fuscous scales present); tarsal segments cream.

Forewing: Length, 18–19.5 mm; ground color rufous; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal elliptical scale patch between R and Cu veins centered with gray; basal half circle scale patch below Cu vein brown bordered by black; antemedial line black, indistinct; claviform spot absent; basal scale patch gray from costa to posterior margin (some rosy scales can be present); gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, white, center light brown, outlined on outer edge with a faint line of brown to dark brown scales, spot surrounded by a larger white trapezoidal field; reniform spot large, oval, cream with center of rufous scales; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line dark reddish brown, scalloped; postmedian band pale gray; black scale patches in middle of cells in postmedian area absent; subterminal line white, curved; apex with a white patch; square to spindle-shaped black to dark reddish brown spots along outer margin; fringe gray. Underside ground color cream with pink along costa; outer margin with black crescent-shaped spots; reniform spot gray.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales; fringe white. Underside ground color white; costal cells C and

Sc cream speckled with pale gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray to cream; venter rufous; disto-lateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa with base straight, broadly curved distally (Figs. 330, 360). Costal process elongate, wide, heavily sclerotized; parallel to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, broad, curved with a decurved apex; extending to just below apex of valve (Figs. 330, 360). Clasper proper absent. Clavus large, club-shaped, base narrower than apex. Sacculus fairly constant throughout length, slightly constricted at two-thirds its length; apex rounded dorsally, truncate ventrally. Valvula wider than valve; well differentiated from valve, apex free; apex round; indentation narrow, deep, ventral margin slightly curved. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus sinuous; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon; a mixture of granular and large spines at apex; dense cornutal patch subapical on vesica; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Head: Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment variably mixed with black and rufous scales, apex cream. Frons with short scales rufous and cream; long scales rufous and cream; lateral spots at eye margin rufous (joined to form a bar); vertex rufous and cream. Antenna filiform; scape rufous and cream; flagellum rufous.

Thorax: Patagium brown with variably distinct black basal band, thin dark rufous median band and a wider white band adjacent to it, thin white apical margin. Tegula light brown and brown (some scales tipped black). Mesothorax light brown and brown scales tipped white and black. Underside of thorax cream. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, light brown and rufous, subapical spot black; first tarsal segment cream, segments 2–5 fuscous with cream apical rings. Mesothoracic femur cream and rufous; tibia cream and rufous (infuscated with black), inner spur more than twice length of outer spur, spurs completely scaled; first tarsal segment cream and rufous, segments 2–5 fuscous basally, rufous medially with cream apical rings. Metathoracic femur cream and rufous; tibia cream, rufous, and fuscous; first tarsal segment cream and rufous, segments 2–5 fuscous basally, rufous medially with cream apical rings.

Forewing: Length, 18.5–21 mm. Ground color brown; basal scale patch small, gray, from midway between M and anal veins to anal vein; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; orbicular spot an oblique trapezoid, white to cream, with a light brown to pale gray center, bordered by a thin line of black scales distally; reniform spot more gray with a light brown to gray apical spot outlined in white; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line black, sinuous, bordered by white below M3 vein; postmedian band less distinct and tending to be more brown; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area.

Abdomen: Dorsum gray; venter cream and rufous. Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin with a wide rectangular notch; ventrolateral invaginated pocket of 8th sternite large, well developed laterally. Ductus bursae moderately elongate (length 2–3 times width); a distinct sclerotized mid-ven-

tral band. Appendix bursae partially sclerotized. Corpus bursae elongate, length greater than twice width; striate convolutions. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; forming greater than a 45 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 112.

Type material.—*Prodenia latifascia* Walker. The type(s): deposited in University Museum, Oxford University, Oxford. Type locality: Jamaica.

Prodenia variolosa Walker. The lectotype ♂ [BMNH, **here designated**] is labeled: St. Domingo, Tweedie, 55-1; *Prodenia variolosa*; Noc. gent. slide No. 3856 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 284. Type locality: St. Domingo, Dominican Republic. The following syntype becomes a paralectotype: ♂, St. Domingo [Dominican Republic], Tweedie, 55-1; *Prodenia, variolosa,* Walker, Paralectotype; E. W. B. Nye 1962. There is no evidence that Nye ever designated a lectotype for *P. variolosa.*

Material Examined.—Specimens were examined from the following countries: Antigua, Bahamas, British Virgin Islands, Costa Rica, Cuba, Dominica, Dominican Republic, El Salvador, Grenada, Guatemala, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Puerto Rico, St. Lucia, United States, Virgin Islands.

Distribution (Fig. 539).—*S. latifascia* is common from the southern United States south to Costa Rica and throughout the Caribbean, except Trinidad.

Discussion.—There is some variation in the intensity of the forewing ground color in both sexes. The amount of brown in the outer border of the hindwing is also somewhat variable with some specimens resembling *S. cosmiodes* and *S. descoinsi.* Sexual dimorphism is present.

Spodoptera cosmiodes (Walker)

Figs. 76, 90, 110, 141, 285–289, 331, 361, 393, 425, 457, 540

Prodenia cosmiodes Walker 1858: 1678.
Spodoptera cosmiodes, Silvain & Lalanne-Cassou 1997: 95.

Diagnosis.—Most similar to *S. latifascia* and *S. descoinsi.* The forewing orbicular spot is more rounded than in *S. descoinsi.* Hindwing with fewer brown scales along outer margin than in *S. latifascia.* Male genitalic differences from *S. latifascia* are: 1) ampulla narrower and apex more produced (compare Figs. 360 and 361), 2) apex of costal process narrower and more recurved (compare Figs. 360 and 361), 3) apex of clavus same diameter as shaft (compare Figs. 360 and 361), and 4) base of vertical projection of juxta narrower (compare Figs. 330 and 331). Female genitalic differences from *S. latifascia* are: 1) distal margin of ventral plate of ostium bursa a circular groove with distal opening narrower than groove (compare Figs. 456 and 457), 2) ductus bursae and corpus bursae narrower, and 3) signum shorter (compare Figs. 424 and 425).

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment a mixture of cream, brown, and black scales. Frons with short scales cream; long scales cream; lateral spots at eye margin black; vertex cream. Antenna filiform; scape cream; flagellum cream.

Thorax: Patagium cream with obscure bands of light brown and white. Tegula cream. Mesothorax cream. Underside of thorax cream. Prothoracic femur cream and rufous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream, subapical spot absent; tarsal segments fuscous, proximal and apical ring cream on segment 1, apical rings on segments 2 and 5 cream, no apical rings on segments 3 and 4. Mesothoracic femur cream; tibia cream, inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings. Metathoracic femur cream; tibia cream; first tarsal segment cream and rufous, remainder fuscous basally, rufous medially with cream apical rings.

Forewing: Length, 16–20 mm; ground color rufous; basal line absent; longitudinal black dash at base absent; R vein not a contrasting color; basal elliptical scale patch between R and Cu veins cream; basal half circle scale patch below Cu vein light brown bordered by dark rufous; antemedial line black, indistinct; claviform spot absent; basal scale patch gray from costa to Cu vein and mostly rosy below Cu vein; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot oval, white, center light brown, outlined on outer edge with a

faint line of brown to dark brown scales, spot surrounded by a larger white trapezoidal field; reniform spot large, oval, cream centered with rufous scales; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line dark reddish brown, scalloped; postmedian band pale gray; black scale patches in middle of cells in postmedian area absent; subterminal line white, curved; apex with a white patch; spindle-shaped to triangular shaped spots along outer margin, indistinct; fringe rufous, brown, and white. Underside ground color cream with light brown scales; outer margin with small black crescent-shaped spots; reniform spot absent.

Hindwing: Ground color white; a small patch of gray scales at apex; fringe white. Underside ground color white; costal cells C and Sc cream speckled with rufous scales (some pale brown); outer margin with a few faint gray spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum cream; venter cream; distolateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa with base straight, broadly curved distally (Figs. 331, 361). Costal process elongate, wide, heavily sclerotized; at base of costa on inner edge; parallel to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, broad, curved with a decurved apex; extending to just below apex of valve (Figs. 331, 361). Clasper proper absent. Clavus large, club-shaped, base narrower than apex. Sacculus fairly constant throughout length, slightly constricted at two-thirds its length; apex rounded dorsally, truncate ventrally. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation narrow, deep, ventral margin slightly curved. Coremata with double lobe, longer lobe elongate, more than 0.5 length of valve, shorter lobe less than half length of longer lobe. Juxta a narrow rectangular band, median process narrow at base and elongate, ventral margin narrowly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus sinuous; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; short, less than 0.75 length of aedoeagus; apicobasal cornutal patch a narrow ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a narrow elongate ribbon; a mixture of granular and large spines at apex; dense cornutal patch subapical on vesica; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Head: Frons with short scales cream and rufous; long scales cream and rufous; vertex light brown and white.

Thorax: Patagium brown with variably distinct black basal band, thin dark rufous median band and a wider white band adjacent, thin white apical margin. Tegula light brown and white (some scales tipped black). Mesothorax light brown and brown scales, some tipped white and light brown. Prothoracic femur rufous and cream; tibia light brown and cream, subapical spot black.

Forewing: Length, 16–19 mm. Basal scale patch small, gray, from midway between M and anal veins to anal vein.

Abdomen: Venter cream (scattered with rufous and brown scales). Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin narrow U-shaped; ventrolateral invaginated pocket of 8th sternite large, well developed laterally. Ductus bursae moderately elongate (length 2–3 times width); completely sclerotized. Appendix bursae completely sclerotized. Corpus bursae elongate, length greater than twice width; striate convolutions. Signum in apical half of corpus bursae; moderately elongate, length between 0.66–1.1 mm; almost vertical.

Larva.—Unknown.

Type material.—*Prodenia cosmiodes* Walker. The lectotype ♂ [BMNH, **here designated**] is labeled: Para. The lectotype is designated to ensure nomenclatural stability in this confusing group of species. Type locality: Para, Brazil.

Material Examined.—Specimens were examined from the following countries: Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guyana, Panama, Paraguay, Peru, Trinidad, Venezuela.

Distribution (Fig. 540).—This species occurs from Panama and Trinidad south to Argentina.

Discussion.—*Spodoptera cosmiodes* is sexually dimorphic. The male differs from the female in the presence of an ochreous patch in the forewing between the antemedial and postmedial lines and below vein M. This patch is larger and more distinct in *S. cosmiodes* than in *S. latifascia* and *S. descoinsi*. There is variation in the amount of ochreous in the ground color of the forewings. Some specimens have almost the entire forewing infuscated with ochreous.

Until recently, *S. cosmiodes* was considered a synonym of *S. latifascia*. *Spodoptera cosmiodes* can be separated from *S. latifascia* by differences in mitochondrial DNA, genital morphology, general color and pattern, and pheromones (Silvain & Lalanne-Cassou 1997). To demonstrate the differences in pheromone blends, Monti *et al.* (1995) calculated the percentage of Z9,E12-14: Ac [(Z,E)-9, 12-tetradecadienyl acetate] relative to the sum of Z9-14: Ac [(Z)-9-tetradecenyl acetate] and Z9,E12-14: Ac ([Z9,E12-14: Ac/(Z9-14: Ac + Z9,E12-14: Ac)] × 100. This percentage averaged 4% for *S. latifascia*, 44.8% for *S. descoinsi* (Monti *et al.* 1995) and 17% for *S. cosmiodes* (Silvain & Lalanne-Cassou 1997).

Spodoptera descoinsi Lalanne-Cassou & Silvain

Figs. 118, 130, 165, 290, 332, 362, 394, 426, 458, 510–512, 540

Spodoptera descoinsi Lalanne-Cassou & Silvain *in* Lalanne-Cassou *et al.* 1994: 28.

Diagnosis.—Most similar to *S. cosmiodes*. Forewing of male with a white, ovate, orbicular spot outlined on outer edge with a faint line of brown to dark brown scales, center light brown, spot surrounded by a larger white trapezoidal field. Female with trapezoidal field less distinct. Male genitalic differences from *S. cosmiodes* are: 1) ampulla wider and apex less decurved (compare Figs. 361 and 362), 2) apex of costal process wider than shaft (compare Figs. 361 and 362), 3) apex of clavus wider than diameter of shaft (compare Figs. 361 and 362), and 4) base of vertical projection of juxta narrower (compare Figs. 331 and 332). Female genitalic differences from *S. cosmiodes* are: 1) distal margin of ventral plate of ostium bursa a narrow U-shape groove with distal opening as wide as groove (compare Figs. 457 and 458) and 2) ductus bursae and corpus bursae wider (compare Figs. 425 and 426).

Description.—Adult Male. *Head:* Basal segment of labial palpus cream with rufous patch that can contain a few black scales; median segment cream and rufous (some specimens mixed with black scales); apical segment cream mixed with rufous scales. Frons with short scales cream; long scales rufous; lateral spots at eye margin absent; vertex rufous and cream. Antenna filiform; scape rufous and cream; flagellum rufous.

Thorax: Patagium rufous with thin basal fuscous transverse band and reddish brown median and apical bands. Tegula light brown and rufous (some scales tipped white, a few black scales along median margin). Mesothorax light brown. Underside of thorax pale rufous to cream. Prothoracic femur rufous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream, rufous, and fuscous, subapical spot black; tarsal segments cream. Mesothoracic femur cream and rufous; tibia rufous and cream, inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings (some specimens are light brown). Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments rufous, fuscous at base with cream apical rings.

Forewing: Length, 15–18 mm; ground color rufous; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal elliptical scale patch between R and Cu veins centered with rufous; basal half circle scale patch below Cu vein brown bordered by black; antemedial line black, indistinct; claviform spot absent; basal scale patch gray from costa to anal vein (indistinct above R vein and can be mixed with dark rosy scales); gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent (only a few scales near reniform spot); orbicular spot oval, white, center light brown, outlined on outer edge with a faint line of brown to dark brown scales, spot surrounded by a larger white trapezoidal field; reniform spot large, a cream oval center with rufous scales; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 continuing down CuA2 vein to postmedial line; postmedial line dark reddish brown, scalloped; postmedian band pale gray; black scale patches in middle of cells in postmedian area absent; subterminal line white, curved; apex with

a white patch (can be reduced to a few white scales in female); square to spindle-shaped black to dark reddish brown spots along outer margin; fringe gray. Underside ground color pale gray and pink; outer margin with black spots; reniform spot gray.

Hindwing: Ground color white; a few pale gray and rufous scales at apex; fringe rufous at apex becoming white toward anal veins. Underside ground color white; costal cells C and Sc white speckled with brown and rufous scales; outer margin with a few faint gray spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum cream; venter cream and rufous; disto-lateral black spots on sternites absent; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa with base straight, broadly curved distally (Figs. 332, 362). Costal process elongate, wide, heavily sclerotized; at base of costa on inner edge; parallel to costa of valve. Cucullus apex round; not produced. Anellifer with lightly sclerotized plate bearing setae absent. Ampulla elongate, broad, curved with a decurved apex; extends to just below apex of valve (Figs. 332, 362). Clasper proper absent. Clavus large, club-shaped, base narrower than apex. Sacculus fairly uniform throughout length, slightly constricted at two-thirds its length; apex rounded dorsally, truncate ventrally. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation narrow, deep, ventral margin slightly curved. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process narrow at base and elongate, ventral margin narrowly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus sinuous; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving dorsally; elongate, greater than length of aedoeagus; apicobasal cornutal patch a narrow ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a wide elongate ribbon; a mixture of granular and large spines at apex; dense cornutal patch on apical diverticulum; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Head: Basal segment of labial palpus rufous, with black scale patch near apex; median segment rufous with black transverse bar at 2/3 length; apical segment rufous, apex cream. Frons with short scales rufous and cream; long scales white; lateral spots at eye margin black; vertex dark reddish brown to black. Antennal scape light brown to reddish brown (can have a few black scales); flagellum reddish brown.

Thorax: Patagium brown with a few black scales basally and indistinct white median and apical bands. Tegula light brown, brown, and white (black scales along median margin). Mesothorax a mixture of light brown, brown, white, and black scales. Underside of thorax white. Prothoracic femur rufous and fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream, rufous, and fuscous, subapical spot black; tarsal segments cream. Mesothoracic femur cream and rufous (some fuscous); tibia rufous and cream, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments rufous, fuscous at base with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments rufous, fuscous at base with cream apical rings.

Forewing: Length, 15–18 mm. Ground color light brown; basal scale patch small, gray, from midway between M and anal veins to anal vein; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; orbicular spot an oblique trapezoid, white to cream, with a light brown to pale gray center, bordered by a thin line of black scales distally; reniform spot brown outlined in white on proximal border, distal apex is a triangular brown spot outlined in white, a white distal border extending to middle; postmedial line black, indistinct, from just below costa to posterior margin, wavy; postmedian band a mixture of gray, brown, and dark pink scales; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area.

Hindwing: Underside outer margin with gray triangular spots in middle of cells Sc to CuA1.

Abdomen: Dorsum cream to rufous; venter

rufous; disto-lateral black spots on sternites (faint to absent). Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin narrow U-shaped; ventrolateral invaginated pocket of 8th sternite large, well developed laterally. Ductus bursae moderately elongate (length 2–3 times width); a distinct sclerotized mid-ventral band. Appendix bursae completely sclerotized. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in apical half of corpus bursae; moderately elongate, length between 0.66–1.1 mm; forming greater than a 45 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 113.

Type material.—*Spodoptera descoinsi* Lalanne-Cassou & Silvain. The holotype ♂ [MNHP] labeled: French Guiana: route de Kaw, pK 45. Type locality: French Guiana: route de Kaw, pK 45.

Material Examined.—Specimens were examined from the following countries: French Guiana, Peru.

Distribution (Fig. 540).—This species is known only from French Guiana and Peru.

Discussion.—There is little variation in the intensity of the ground color of the forewing. Sexual dimorphism is present, but the size of the ochreous patch in the forewing of the male is less than in *S. cosmiodes* and *S. latifascia. Spodoptera descoinsi* is smaller than either *S. cosmiodes* or *S. latifascia.*

Spodoptera praefica (Grote)

Figs. 46, 155–156, 291–292, 333, 363, 395, 427, 459, 513–515, 541

Prodenia praefica Grote 1875: 44; Smith 1891: 45; Smith 1893: 170; Grote 1895: 43; Dyar 1903: 13 (subspecies of *ornithogalli*); Barnes & McDunnough 1917: 67; Draudt 1926: 256; McDunnough 1938: 96.

Spodoptera praefica; Todd & Poole 1980: 728; Franclemont & Todd 1983: 141; Poole 1989: 925; Poole & Gentili 1996: 774.

Diagnosis.—Resembles the female of *S. ornithogalli.* Hindwing underside of *S. praefica* with distinct crescent-shaped spot at base of Cu veins, can be seen as a faint spot on upperside. Male genitalia with coremata reduced, closely appressed to sacculus (Fig. 363). Female genitalia with ventral plate of ostium bursa wider than high (Fig. 459); signum short (Fig. 427).

Description. Adult Male.—*Head:* Basal segment of labial palpus black with longer ventral scales cream; median segment black, variably mixed with brown and cream, apex cream (with a few rufous scales); apical segment black, apex cream. Frons with short scales cream; long scales cream to light brown; lateral spots at eye margin black; vertex cream, light brown, and brown. Antenna filiform; scape cream and brown; flagellum cream and brown.

Thorax: Patagium light brown flecked with black, median transverse band white. Tegula light brown. Mesothorax light brown with a few black tipped scales. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; tarsal segments cream and fuscous. Mesothoracic femur cream and fuscous; tibia cream and fuscous, inner spur more than twice length of outer spur, spurs completely scaled; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and fuscous; tibia cream and fuscous; tarsal segments cream, fuscous at base on segments 2–4, sometimes on 1.

Forewing: Length, 15–17 mm; ground color brown; basal line absent; longitudinal black dash at base absent; R vein not a contrasting color; basal triangular scale patch between R and Cu veins brown bordered by white (can be mixed with black scales); basal half circle scale patch below Cu vein light brown bordered by black; antemedial line absent; claviform spot absent; basal scale patch from costa to below anal vein; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot an oblique trapezoid, cream, with a light brown center bordered by black; reniform spot indistinct, brown with black scales, white and black on proximal border, apex light brown bordered by a white V-shaped mark; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line indistinct, white bordered by a few black scales; postmedian band gray; black scale patches short in middle of cells R4 to CuA1 in postmedian area; subterminal line white, curved; apex lacking a white patch (some specimens can have more white scales creating an indistinct patch); black crescent-shaped spots along outer

margin; fringe light brown (tipped brown). Underside ground color pale gray; outer margin with black spots; reniform spot gray.

Hindwing: Ground color white suffused with pale gray; apex, outer margin, and veins with pale gray scales; fringe white. Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; crescent-shaped gray spot at base of Cu veins.

Abdomen: Dorsum pale gray; venter cream and gray; disto-lateral black spots on sternites; 8th tergite with spiculate patches absent on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 333, 363). Costal process medium length and width; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate, slightly curved with a decurved apex; extends beyond apex of valve (Figs. 333, 363). Clasper proper absent. Clavus short, round, covered with setae. Sacculus widest at one-third its length, distal half narrow, constant width; apex truncate. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation small, ventral margin slightly curved. Coremata reduced, closely appressed to sacculus; no distinct lobes. Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch quadrate; length moderate, extending to before middle of vesica; cornuti a mixture of small and large spines; lateral cornutal patch an ovate area; composed of large spines; dense cornutal patch dorsolaterally; distal cornutus a bulbous elliptical plate, apex pointed.

Adult Female.—Essentially as described for male except:

Forewing: Length, 15–18 mm.

Abdomen: Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin slightly concave; ventrolateral invaginated pocket of 8th sternite small, more developed ventrally than laterally. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in apical half of corpus bursae; short, length less than 0.65 mm; forming greater than a 45 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 114.

Type material.—*Prodenia praefica* Grote. The lectotype ♂ [BMNH, **here designated**] is labeled: 5568, Calif.; California, Grote Coll., 82-54; *Prodenia, praefica,* Grote type; Noc. gent. slide No. 3947 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 291. Type locality: California, USA. The following syntypes become paralectotypes: (1) Label data: 5568, Calif.; California, Grote Coll., 82-54; *Prodenia, praefica,* Grote. (2) Label data: Grote Coll., 82-54; California, Mendocino, vi. 72.

Material Examined.—Specimens were examined from the following country: United States.

Distribution (Fig. 541).—This species is restricted to the western United States from Washington, Oregon, and California, east to western Montana, southwestern Colorado, and Utah.

Discussion.—There is some variation in the intensity of the forewing color and pattern. Unlike *S. ornithogalli*, there is no sexual dimorphism. The valve and sacculus width of the male genitalia are narrower than in *S. ornithogalli.* The coremata are reduced and closely appressed to the sacculus with no distinct lobes; in *S. ornithogalli* the coremata are large with two distinct lobes. The ventral plate of ostium bursa of the female genitalia is square in *S. praefica* and rectangular in *S. ornithogalli.* The signum is reduced in *S. praefica* and elongate in *S. ornithogalli.*

Spodoptera marima (Schaus)

Figs. 293–295, 334, 364, 396, 428, 460, 542

Prodenia marima Schaus 1904: 150; Draudt 1926: 256.
Spodoptera marima; Todd & Poole 1980: 728; Poole 1989: 924.

Diagnosis.—Resembles females of *S. ornithogalli*, but *S. marima* is not sexually dimorphic; and the forewing length is shorter. Male genitalia with costal lobe of sacculus less robust with a more pointed apex than in *S. ornithogalli* (compare Figs. 364 and 365). Female genitalia with fine dense scales on 8th segment gray to brown.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment black, apex cream. Frons with short scales rufous and cream; long scales cream; lateral spots at eye margin black; vertex cream, light brown, and brown. Antenna filiform; scape cream to light brown; flagellum cream annulated brown, becoming completely cream toward apex.

Thorax: Patagium light brown mixed with white scales to brown with scales tipped white, a basal patch, thin median band, and subapical scales black, thin apical margin white. Tegula light brown to brown (fuscous and black scales forming indistinct transverse banding). Mesothorax light brown to brown with variable mix of white and fuscous scales. Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot black; tarsal segments 1–2, 5 cream, segments 3–4 fuscous. Mesothoracic femur cream and fuscous; tibia fuscous and cream, inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and fuscous; tibia cream and fuscous; tarsal segments cream, segments 2–5 pale fuscous at base.

Forewing: Length, 12–14 mm; ground color dark brown; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal elliptical scale patch between R and Cu veins centered with gray; basal half circle scale patch below Cu vein brown bordered by black; antemedial line black, indistinct; claviform spot absent; basal scale patch gray from costa to anal vein (indistinct above Cu vein); gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent (only a few scales near reniform spot); orbicular spot an oblique trapezoid, white to cream, with a light brown to pale gray center, bordered by a thin line of black scales distally; reniform spot black outlined in white on proximal border, distal apex is a triangular gray to light brown spot outlined in white, a white distal border extending to middle; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line indistinct, black bordered by white below M3 vein; postmedian band gray; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area; subterminal line white, curved; apex with a few white scales, no distinct patch; black crescent-shaped spots along outer margin (some specimens are more square to spindle-shaped); fringe gray. Underside ground color pale gray; outer margin with black crescent-shaped spots; reniform spot gray.

Hindwing: Ground color white; a small patch of gray scales at apex; fringe white. Underside ground color white; costal cell C cream and Sc cell white, speckled with gray scales; outer margin with a few faint gray spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum cream to pale gray; venter cream and gray; disto-lateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 334, 364). Costal process elongate, narrow; at base of costa on inner edge; parallel to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate, slightly curved with a decurved apex; extending to just below apex of valve (Figs. 334, 364). Clasper proper absent. Clavus short, round, covered with setae. Sacculus widest at one-third its length, distal half narrow, constant width; apex truncate. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation small, ventral margin slightly curved. Coremata elongate, more than 0.5 length of valve; in form of a double lobe.

Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica perpendicular to aedoeagus; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch quadrate; short, extending just beyond apex of aedoeagus; cornuti composed of short spines; lateral cornutal patch absent; dense cornutal patch dorsolaterally; distal cornutus an ovate plate with large spines at apex.

Adult Female.—Essentially as described for male except:

Forewing: Length, 13–15 mm.

Abdomen: Fine dense scales on 8th segment cream.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin U-shaped; ventrolateral invaginated pocket of 8th sternite absent. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae completely sclerotized. Corpus bursae bulbous, length less than twice width; smooth. Signum in apical half of corpus bursae; short, length less than 0.65 mm; almost vertical.

Larva.—Unknown.

Type material.—*Prodenia marima* Schaus. The holotype ♂ [USNM] is labeled: Paraná, Castro; Collection, Wm Schaus; Type, 10527, U.S.N.M. [red label]; *Prodenia, marima,* Type Schs [hand written]; USNM ENT 00142009 [bar code label]. Type locality: Castro, Paraná, Brazil.

Material Examined.—Specimens were examined from the following countries: Bolivia, Brazil, Colombia, Ecuador, French Guiana, Venezuela.

Distribution (Fig. 542).—*Spodoptera marima* ranges from Colombia, Venezuela, and French Guiana, south to Amazonian Ecuador and Paraná, Brazil.

Discussion.—*S. marima* is very similar to *S. ornithogalli*, but their ranges are disjunct. *Spodoptera marima* is slightly smaller and the forewing pattern is not as well developed as in *S. ornithogalli*. The hindwing is almost immaculate white and lacks the brown apical border of *S. ornithogalli*. In the female, the hair tuft on the neck of the ovipositor is gray to brown compared to black in *S. ornithogalli*.

Spodoptera ornithogalli (Guenée)

Figs. 35, 81, 128, 154, 157, 296–299, 335, 365, 397, 429, 461, 516–518, 542

Prodenia ornithogalli Guenée *in* Boisduval & Guenée 1852a: 163; Walker 1856: 193; Smith 1891: 45; Smith 1893: 169; Grote 1895: 42; Dyar 1903: 123; Barnes & McDunnough 1917: 67; Draudt 1926: 256; McDunnough 1938: 96.

Prodenia eudiopta Guenée *in* Boisduval & Guenée 1852a: 164; Walker 1856: 193.

Prodenia flavimedia Harvey 1875: 274 [synonymized by Hampson 1909: 248].

Prodenia lineatella Harvey 1875: 275.

Prodenia praefica form *eudioptoides* Barnes & Benjamin 1923: 81; [synonymized by McDunnough 1943: 1].

Spodoptera ornithogalli; Todd and Poole 1980: 728; Franclemont & Todd 1983: 141; Poole 1989: 925; Poole & Gentili 1996: 774.

Diagnosis.—Similar to *S. latifascia, S. marima,* and *S. pulchella,* but *S. ornithogalli* is sexually dimorphic. Can be confused with the female of *S. latifascia,* but forewing with crescent-shaped spots of adterminal line not joined with adjacent spots to form spindle-shaped spots as in *S. latifascia.* Length to width ratio of forewing is less than 2.5, in *S. latifascia* ratio is greater than 2.5. Lacks well defined white line along Cu vein from antemedial to postmedial line as in *S. pulchella* (compare Figs. 296–299 and 300). *Spodoptera marima* is smaller, not sexually dimorphic, its hindwings are pure white, and it is geographically isolated from *S. ornithogalli.* Male genitalia of *S. ornithogalli* resemble those of *S. marima,* but in *S. ornithogalli* the apex of valvula is truncate and in *S. marima* it is more pointed (compare Figs. 364 and 365). Female genitalia of *S. ornithogalli* resemble those of *S. marima,* but in *S. ornithogalli* striations in corpus bursae are less convoluted, the signum is shorter (compare Figs. 428 and 429), and fine dense scales on 8th segment are black.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales; apical segment black, apex cream. Frons with short scales cream; long scales rufous; lateral spots at eye margin black (can form into a bar); vertex rufous (variably mixed with brown). Antenna filiform; scape cream; flagellum cream.

Thorax: Patagium light brown mixed with brown scales, some tipped white, transverse rows of black scales (dark scales can be replaced by white ones in some specimens). Tegula light brown and brown (dark scales can be absent). Mesothorax light brown (dark scales can be absent). Underside of thorax white. Prothoracic femur fuscous and cream; tibia with lateral scale tufts not extending beyond first tarsal segment, cream and fuscous, subapical spot absent; tarsal segments fuscous with cream apical rings.

Mesothoracic femur fuscous and cream; tibia fuscous and cream, inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments fuscous with cream apical rings. Metathoracic femur fuscous and cream; tibia fuscous and cream; tarsal segments fuscous with cream apical rings.

Forewing: Length, 15–17 mm; ground color brown; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal elliptical scale patch between R and Cu veins centered with gray; basal half circle scale patch below Cu vein brown bordered by black; antemedial line black, indistinct; claviform spot absent; basal scale patch gray from costa to anal vein (indistinct above Cu vein); gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent (only a few scales near reniform spot); orbicular spot an oblique trapezoid, cream, with a light brown center bordered by light brown to black; reniform spot black to brown outlined in white on proximal border, distal apex is a triangular light brown spot outlined in white, a white distal border extending to middle; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line indistinct, black bordered by white below M3 vein; postmedian band pale gray to gray with an elliptical gray to brown spot along subterminal line; black scale patches in middle of cells M2 to CuA1 in postmedian area; subterminal line white, curved; apex with a white patch; black crescent-shaped spots along outer margin; fringe gray. Underside ground color pale gray; outer margin with black crescent-shaped spots; reniform spot gray.

Hindwing: Ground color white; apex, outer margin, and veins with light brown scales; fringe white (some specimens have a line of light brown running through fringe). Underside ground color white; costal cells C and Sc white speckled with gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray to cream; venter cream and rufous; disto-lateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 335, 365). Costal process, elongate, narrow; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate; slightly curved with a decurved apex; extending to just below apex of valve (Figs. 335, 365). Clasper proper absent. Clavus short, round, covered with setae. Sacculus widest at one-third its length, distal half narrow, uniform in width; apex truncate. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation small, ventral margin slightly curved. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica perpendicular to aedoeagus; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch quadrate; short, extending just beyond apex of aedoeagus; cornuti composed of short spines; lateral cornutal patch absent; dense cornutal patch dorsolaterally; distal cornutus an ovate plate with large spines at apex.

Adult Female.—Essentially as described for male except:

Forewing: Length, 14–19 mm. R vein not a contrasting color; basal half circle scale patch below Cu vein gray bordered by black; gray patch covering anal cell and half of cell CuA2 absent; curved white line from antemedial line to postmedial line

absent; orbicular spot an oblique trapezoid, white to cream, with a light brown to pale gray center, bordered by a thin line of black scales distally; reniform spot more gray with a light brown to gray apical spot outlined in white; postmedian band less distinct and tends to be more brown; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area.

Abdomen: Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin U-shaped; ventrolateral invaginated pocket of 8th sternite large, well developed laterally. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; a few striae. Signum at middle of corpus bursae; moderately elongate, length between 0.66–1.1 mm; almost vertical.

Larva.—See description, p. 114.

Type material.—*Prodenia ornithogalli* Guenée. The holotype ♀ [USNM] labeled: "Ex. Musaeo, Ach. Guenée; Oberthur Collection (yellow label, red rectangle with red letters); 1.2 Pr. Ornithogalli Gn., Spec. 258., 1.Amér. Sept. Jouncé par M. Bdval., 2. Brésil ?, [next 3 lines illegible] (hand written label)"; North America. Type locality: North America.

Prodenia eudiopta Guenée. The type repository is unknown. Type locality: North America.

Prodenia flavimedia Harvey. The lectotype ♂ [BMNH, **here designated**] is labeled: Syntype, Grote Coll. 82-54; U. S. America; *Prodenia, flavimedia,* Type Harvey; Noc. gent. slide No. 3943 ♂. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 298. Type locality: USA.

Prodenia lineatella Harvey. The lectotype ♀ [BMNH, **here designated**] is labeled: Syntype, Grote Coll. 82-54; U. S. America; *Prodenia, lineatella,* Type Harvey; Noc. gent. slide No. 3942 ♀. The lectotype is designated to ensure nomenclatural stability in this confusing group of species and is illustrated in Fig. 299. Type locality: USA.

Prodenia praefica form *eudioptoides* Barnes & Benjamin. The holotype ♂ [USNM] labeled: San Diego, Calif.; Aug. 26 '21 (hand written); *P. praefica, eudioptoides,* Holotype ♂ B & Benj. (hand written, bordered with red and with red lines). Type locality: San Diego, California, USA.

Material Examined.—Specimens were examined from the following countries: Antigua, Bermuda, Canada, Costa Rica, Cuba, Dominica, Dominican Republic, Guatemala, Honduras, Mexico, Puerto Rico, United States.

Distribution (Fig. 542).—This species has been collected throughout North America from southern Canada to Florida and west to California. Data in the USNM report it from 34 of the 48 continental states. It probably occurs in the other 14 states, but has not been collected. Numerous specimens were collected in Bermuda (Ferguson *et al.* 1991). It is found in the Greater Antilles, except Jamaica, and in the Lesser Antilles to Dominica. *Spodoptera ornithogalli* occurs in Mexico south to Guatemala and Costa Rica.

Discussion.—There is variation in the extent of the ochreous patch in the median area of the forewing in the male. Some specimens lack this patch, resembling the female.

In central California, the female of *S. ornithogalli* is similar to *S. praefica,* but is easily separated by the lack of a central spot on the underside of the hindwing.

Spodoptera pulchella (Herrich-Schäffer)

Figs. 75, 88, 119, 162, 300, 336, 366, 398, 430, 462, 519–521, 543

Laphygma pulchella Herrich-Schäffer 1868: 116.
Prodenia exquisita Möschler 1886: 41.
Prodenia pulchella; Draudt 1926: 255.
Spodoptera pulchella; Todd and Poole 1980: 730; Franclemont & Todd 1983: 141; Poole 1989: 925; Poole & Gentili 1996: 774.

Diagnosis.—Most similar to the female of *S. ornithogalli.* Forewing with a broad white line running along Cu vein from antemedial to postmedial line (Fig. 300), and male genitalia with apex of sacculus closer to apex of valve than in *S. ornithogalli*; coremata with 2 lobes of almost equal size (compare Figs. 365 and 366). Female genitalia with corpus bursae round and striations straight (Fig. 430); fine dense scales on 8th segment gray.

Description. Adult Male.—*Head:* Basal segment of labial palpus cream with median patch variably mixed with black and rufous scales; median segment cream with black median band variably mixed with rufous scales (black markings can be weakly developed); apical segment cream mixed with rufous scales. Frons with short scales cream; long scales cream and rufous, or

light brown; lateral spots at eye margin rufous (can form into a bar); vertex cream (suffused with brown or rufous). Antenna filiform; scape cream; flagellum cream.

Thorax: Patagium brown with variably distinct black basal band, thin dark rufous median band and a wider white band adjacent to it, thin white apical margin. Tegula with longer scales around edge brown to dark rufous, with oblique banding of black, brown, and white. Mesothorax light brown and white. Underside of thorax white to cream. Prothoracic femur cream and rufous; tibia with lateral scale tufts not extending beyond first tarsal segment, cream (can have fuscous scales present), subapical spot black; tarsal segments cream. Mesothoracic femur cream and rufous; tibia cream and rufous (infuscated with black), inner spur more than twice length of outer spur, mediolateral surface broadly devoid of scales on both spurs; tarsal segments cream. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments cream.

Forewing: Length, 14–15 mm; ground color brown; basal line absent; longitudinal black dash at base absent; R vein from base to reniform spot gray; basal triangular scale patch between R and Cu veins gray bordered by cream on apical end; basal half circle scale patch below Cu vein light brown bordered by black; antemedial line absent; claviform spot absent; basal scale patch small, gray, from midway between M and anal veins to anal vein; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line bordered by black along posterior margin; orbicular spot an oblique trapezoid, white to cream, with a light brown to pale gray center, bordered by a thin line of black scales distally; reniform spot brown in basal half, apical half elongate, white, centered with light brown, outlined in black; white scales along Cu vein from orbicular spot to junction of veins M3 and CuA1 which extend down veins M3, CuA1, and CuA2 to postmedial line; postmedial line black, sinuous, bordered by white below M3 vein; postmedian band with an elliptical brown spot along subterminal line; black scale patches in middle of cells R4 to CuA2, patch in R4 basal to other patches, patch in R5 consisting of only a few scales in postmedian area; subterminal line white, curved; apex with a white patch; black crescent-shaped spots along outer margin; fringe gray. Underside ground color light brown to pale gray; outer margin with black crescent-shaped spots; reniform spot gray.

Hindwing: Ground color white; apex, outer margin to vein CuA2, and distal ends of veins Rs to CuA2 with light brown scales; fringe rufous at apex becoming white toward anal veins. Underside ground color white; costal cells C and Sc cream speckled with brown scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray; venter cream and rufous; disto-lateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus curved in apical half; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa slightly bent at middle (Figs. 336, 366). Costal process, elongate, narrow; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate, slightly curved with a decurved apex; extending to just below apex of valve (Figs. 336, 366). Clasper proper absent. Clavus short, round, covered with setae. Sacculus widest at one-third its length, distal half narrow, constant width; apex truncate. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation small, ventral margin slightly curved. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum equal in diameter to shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica perpendicular to aedoeagus; moderately elongate, 0.75–1.0 length of aedoeagus; apicobasal cornutal patch quadrate; short, extending just beyond apex of aedoeagus; cornuti composed of short spines; lateral cornutal patch an ovate area; composed of large spines; dense cornutal patch subapical on vesica; distal cornutus an ovate plate with large spines at apex.

Adult Female.—Essentially as described for male except:

Forewing: Length, 13–17 mm.

Abdomen: Fine dense scales on 8th segment gray.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin Ushaped; ventrolateral invaginated pocket of 8th sternite large, well developed laterally. Ductus bursae short (length less than twice width); completely sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; forming less than a 30 degree angle to vertical axis of corpus bursae.

Larva.—See description, p. 115.

Type material.— *Laphygma pulchella* Herrich-Schäffer. The syntypes are deposited in Museo Zoologico Cubano, Havana, Cuba. Type locality: Havana; Cuba.

Prodenia exquisita Möschler. The syntypes are in Museum für Naturkunde der Humboldt University, Berlin. Type locality: Jamaica.

Material Examined.—Specimens were examined from the following countries: Bahamas, Cayman Islands, Cuba, Dominican Republic, Jamaica, Puerto Rico, United States.

Distribution (Fig. 543).—This is an uncommon species that occurs from the Florida Keys and Bahamas, south to Cuba, Cayman Islands, and Jamaica, and east to the Dominican Republic and Puerto Rico.

Discussion.—There is insignificant variation and no sexual dimorphism in *S. pulchella*. *Spodoptera pulchella* resembles females of *S. ornithogalli*, but *S. pulchella* can be distinguished by the curved white line along the Cu vein from the antemedial to postmedial line. The coremata in the male genitalia have 2 large lobes of almost equal length. The corpus bursae in the female genitalia is larger and the signum is more horizontal than in *S. ornithogalli*.

S. pulchella is known in the United States only from Florida. The earliest record is from Big Pine Key in the southern end of the Florida Keys collected in 1976. By 1989 it had spread as far north as Homestead, Dade County in southern Florida.

Spodoptera roseae (Schaus)

Figs. 27, 94, 140, 301–303, 337, 367, 399, 431, 463, 543

Trachaea [sic] *roseae* Schaus 1923: 33.
Laphygma roseae; Richards 1941: 239.
Spodoptera roseae; Linsley & Usinger 1966: 160; Hayes 1975: 176; Todd & Poole 1980: 733; Poole 1989: 925.

Diagnosis.—*S. roseae* is endemic to the Galapagos Islands and cannot be confused with other species found there. The male antenna is serrate (Fig. 20); all other New World *Spodoptera* have filiform antennae (Fig. 18). Forewing ground color is brown with a brown patch along the subterminal line. The male genitalia have the ampulla extending to just below the apex of the valve (Fig. 367); coremata in form of a double lobe with dorsal lobe more than half the length of ventral lobe. The distal margin of the ventral plate of the ostium bursa is slightly concave (Fig. 463).

Description. Adult Male.—*Head:* Basal segment of labial palpus black; median segment dark gray to two-thirds length, apical third mixed rufous and cream (apical third can be light gray); apical segment dark gray. Frons with short scales rufous and cream; long scales rufous; lateral spots at eye margin black; vertex brown and cream. Antenna serrate; scape cream and brown; flagellum cream and brown.

Thorax: Patagium brown with thin white apical margin. Tegula brown (some scales tipped white). Mesothorax brown with some scales tipped white. Underside of thorax cream. Prothoracic femur fuscous; tibia with lateral scale tufts not extending beyond first tarsal segment, fuscous and cream, subapical spot absent; tarsal segments fuscous with cream apical rings. Mesothoracic femur cream and rufous; tibia cream and rufous, inner spur less than twice length of outer spur, internal surface at base thinly devoid of scales on large spur; tarsal segments fuscous with cream apical rings. Metathoracic femur cream and rufous; tibia cream and rufous; tarsal segments fuscous with cream apical rings.

Forewing: Length, 20–22 mm. Ground color dark grayish brown; basal line absent; short longitudinal black dash at base of Cu vein; R vein not a contrasting color; basal scale patch between R and Cu veins absent; basal half circle scale patch below Cu vein absent; antemedial line black; claviform spot absent; basal scale patch absent; gray patch covering anal cell and half of cell CuA2 absent; oblique brown mark from fifth outer marginal spot to vein CuA2 absent; curved white line from antemedial line to postmedial line absent; orbicular spot round, cream, with buff to brown center, outlined in black; reniform spot cream out-

lined in black, center light brown to brown; white scales along Cu vein and bases of M3 and CuA1 veins absent; postmedial line black, from just below costa to posterior margin, wavy; postmedian band with an indistinct, round, black spot along subterminal line; subterminal line white, indistinct; apex lacking a white patch; black trapezoidal-shaped spots along outer margin; fringe brown. Underside ground color pale gray; outer margin with black spots; reniform spot darker, indistinct.

Hindwing: Ground color pale gray; gray scales along apex and outer margin; fringe white with gray median line to vein CuA2. Underside ground color pale gray; costal cells C and Sc white speckled with gray scales; outer margin with gray triangular spots in middle of cells Sc to CuA1; no spot on underside.

Abdomen: Dorsum pale gray; venter pale gray; disto-lateral black spots on sternites; 8th tergite with spiculate patches present on caudal margin.

Genitalia: Uncus evenly curved; slender, gradually narrowing toward pointed apex; setae absent or few. Scaphium elongate, weakly developed. Tegumen lacking a pair of projecting arms on upper third. Costa straight (Figs. 337, 367). Costal process narrow, elongate; at base of costa on inner edge; perpendicular to costa of valve. Cucullus apex truncate; not produced. Anellifer with lightly sclerotized plate bearing setae present. Ampulla elongate, slightly curved with a decurved apex; extending to just below apex of valve (Figs. 337, 367). Clasper proper absent. Clavus short, round, covered with setae. Sacculus widest at one-third its length, distal half narrow, constant width; apex truncate. Valvula wider than valve; well differentiated from valve, apex free; apex truncate; indentation narrow, deep, ventral margin slightly curved. Coremata elongate, more than 0.5 length of valve; in form of a double lobe. Juxta a narrow rectangular band, median process moderately broad at base and elongate, ventral margin broadly concave. Anellus with minute granules. Vinculum U-shaped with parallel arms and a robust base. Aedoeagus straight; coecum smaller in diameter than shaft; patch of spines absent on apex of membranous sheath surrounding aedoeagus. Vesica curving ventrally; elongate, greater than length of aedoeagus; apicobasal cornutal patch a wide ribbon; length moderate, extending to before middle of vesica; cornuti in form of minute flat granules; lateral cornutal patch a wide elongate ribbon; a mixture of granular and large spines at apex; dense cornutal patch subventrally on vesica; distal cornutus an ovate plate with large spines at apex.

Adult Female.—Essentially as described for male except:

Head: Antenna filiform.

Forewing: Length, 20–22 mm.

Abdomen: Fine dense scales on 8th segment black.

Genitalia: Ventral plate of ostium bursa with height greater than width; distal margin slightly concave; ventrolateral invaginated pocket of 8th sternite small, more developed ventrally than laterally. Ductus bursae short (length less than twice width); partially sclerotized. Appendix bursae partially sclerotized. Corpus bursae bulbous, length less than twice width; striate convolutions. Signum in apical half of corpus bursae; elongate, length greater than 1.15 mm; forming greater than a 45 degree angle to vertical axis of corpus bursae.

Larva.—Unknown.

Type material.—*Trachaea* [sic] *roseae* Schaus. The holotype ♂ [USNM] is labeled: Conway Bay; Indefatigable; Galapagos; April 1 1933. Type No. 26507; U.S.N.M. [red label]. *Trachea; roseae;* type Schs [hand written in black ink]. ♂ genitalia on; slide Aug. 1966; E.L.T. 2341. Genitalia Slide; By ELT ♂; USNM 46620 [green label]. Type locality: Galapagos: Indefatigable, Conway Bay.

Material Examined.—Specimens were examined from the following country: Ecuador (Galapagos Islands).

Distribution (Fig. 543).—*S. roseae* is endemic to the Galapagos Islands where it occurs on the following islands: Isabela, Santa Cruz, Santiago, Marchena, and Pinta.

Discussion.—There is slight variation in the forewing ground color ranging from a dark grayish brown to brown. There is no sexual dimorphism. The antenna of the male are serrate, a character state shared only with *S. cilium.* The serrations in *S. roseae* are more developed than in *S. cilium.*

LARVAL SYSTEMATIC TREATMENT

The majority of *Spodoptera* are economic pests of various food and horticultural crops throughout the world. Of the 30 species of *Spodoptera,* larvae are known for 20. Specimens of *S. cilium, S.*

pecten, and *S. triturata* were not available, but I have include descriptions taken from the literature.

Two groups of workers will be interested in identifying larvae, those that are field collecting live material and those working with preserved specimens in museum collections. Therefore, two descriptions are included for each species, one for preserved larvae and one based on color compiled from the literature based on living specimens.

There is considerable variation in the color and pattern of various markings in *Spodoptera* larvae. Characters used include some morphological structures such as mandible form, number of crochets, and ratio of ecdysial line to frons height. These characters are of some use, but one must still resort to the pattern of various markings found on the head, thorax, and abdomen. The key uses both morphological and pattern characters to help differentiate between the species. It may not be possible to identify all *Spodoptera* larvae using this key.

Many keys to local faunas have been published. Most North American species were treated by Levy & Habeck (1976). Other keys to the North American fauna were those by Crumb (1927, 1956). Passoa (1991) treated common species from Honduras, and this work can also be useful to both Nearctic and Neotropical workers. Keys to African species can be found in Blair (1974) and Brown & Dewhurst (1975). Zimmerman (1958) included a key to the Hawaiian species.

Illustrations of various parts of *Spodoptera* larvae can be found in Crumb (1927), van den Bosch & Smith (1955), Tanada & Beardsley (1958), Angulo & Weigert (1975), and Brown & Dewhurst (1975). Crumb (1929) and Levy & Habeck (1976) illustrated larvae with black and white photographs. Color illustrations can be found in Fletcher (1914), Faure (1943), and Holloway (1989). Color photographs of larvae can also be found in Passoa (1991). Color photographs of Australian *Spodoptera* can be found on the Lepidoptera of Australia Website (http: //linus.socs.uts.edu.au/ ~don/larvae/larvae.html).

Due to the variation in markings and coloration of *Spodoptera* larvae, identifications in the literature pertaining to plant hosts should be viewed with caution.

KEY TO *SPODOPTERA* LARVAE

1. Segmental spots uniform in size on abdominal segments 1–8 (Fig. 144) 2
1′. Segmental spots on abdominal segments 7 and 8 larger than those on 1–6 (Fig. 145) 4
1″. Segmental spots equal in size on abdominal segments 1 and 8, smaller on 2–6 (Fig. 477–479); spiracular band interrupted by a spot on abdominal segment 1 (Fig. 148) ..... *S. eridania*
1*. Segmental spots on abdominal segments 6–8 gradually increasing in size (Fig. 149) ..... *S. androgea*
1**. Segmental spots on abdomen absent (Fig. 150), faint (Fig. 151), or can be present in dark forming of *S. exigua* (Fig. 152); (if present, abdominal segments 2–6 without lateral dark spots in spiracular band) .. 6
2(1). Segmental spots with a distinct white spot medially to near apex (Fig. 144) ..... *S. albula*
2′. Segmental spots with a line passing through them (Figs. 154–155) 3
2″. Segmental spots lacking contrasting marks (Figs. 488, 505) 8
3(2′). Segmental spots on segments 1–6, almost extending to middorsal stripe (Fig. 155); mesothorax with lateral dark spot present (Fig. 156); metathorax with segmental spot rectangular (Fig. 156) .... *S. praefica*
3′. Segmental spots on segments 1–6, extending no more than half the distance between dorsolateral and middorsal stripes (Fig. 154); mesothorax with lateral dark spot absent (Fig. 157); metathorax with segmental spot in form of an elongate, narrow rectangle (Fig. 516) ..... *S. ornithogalli*
4(1′). Segmental spots with a distinct white spot near apex (Fig. 158); segments 1–6 in spiracular band with a white or light colored spot caudal to spiracle (Fig. 159) ..... *S. litura*
4′. Segmental spots lacking contrasting marks (Fig. 160) ..... *S. dolichos*
4″. Segmental spots with a dotted line along anterior margin (Fig. 161) 5
4*. Segmental spots with narrow white dashes (Fig. 162); segments 1–6 on spiracular band with a white or light colored spot caudal to spiracle (Fig. 159) ..... *S. pulchella*
4**. Segmental spots with a white spot mid-basally (Fig. 163); segments 1–6 in spiracular band with a white or light colored spot caudal to spiracle (can be indistinct) (Fig. 159) ..... *S. littoralis*

5(4″). Ratio of ecdysial line: frons height, averages less than 0.62 (Fig. 166); frons yellowish brown; head not reticulate (Fig. 164) ..... *S. latifascia*

5′. Ratio of ecdysial line: frons height, averages between 0.63–0.84 (Fig. 166); frons dark brown; head reticulate (Fig. 165) ..... *S. descoinsi*

6(1**). Ratio of ecdysial line: frons height, averages less than 0.62 (Fig. 166); spiracles not stalked ..... *S. exigua*

6′. Ratio of ecdysial line: frons height, averages between 0.63–0.84 (Fig. 166); spiracles stalked (Fig. 167) ..... *S. pectinicornis*

6″. Ratio of ecdysial line: frons height, averages greater than 0.88 (Fig. 166); spiracles not stalked 7

7(6″). Cutting edge of mandible serrate (Fig. 168); body with pavement granules; body setal pinacula large (Fig. 150) ..... *S. frugiperda*

7′. Cutting edge of mandible chisel-like, teeth not distinct (Fig. 169); body smooth; body setal pinacula minute ..... *S. exempta*

8(2″). Cutting edge of mandible chisel-like, teeth not distinct (Fig. 169); total number of crochets on prolegs 3–6 and 10 on one side of body less than 107 ..... *S. mauritia*

8′. Cutting edge of mandible serrate, teeth distinct (Fig. 168); total number of crochets on prolegs 3–6 and 10 on one side of body greater than 107 ..... *S. picta*

Larval Descriptions

Spodoptera exigua (Hübner)

Figs. 151–152, 471–473

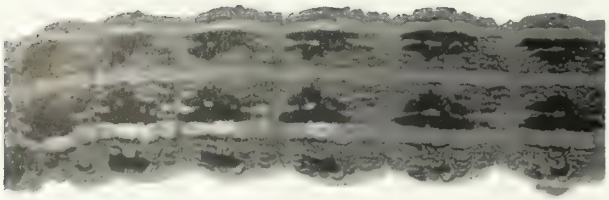
Diagnosis.—General ground color is variable and can be yellow, green, or brown. Head color can be pale (yellow or green) to brown, with dark submedial reticulate patterns on pale heads and light reticulations on dark heads. The body is usually patterned with white dots and short lines. Paired dorsal markings on mesothorax round when present. The dark triangular subdorsal markings common in most species of *Spodoptera* are usually absent, if present, they are not triangular, but more elongate or round (Levy & Habeck 1976).Total number of crochets on all 5 pairs of prolegs on one side of body is less than 106.

Description of preserved specimens.— *Head:* Color pale to black; reticulate; frons pale to black; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages less than 0.62. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax segmental spot absent (can be present in heavily marked specimens (Levy & Habeck 1976)); with lateral dark spot present. Metathorax with segmental spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots on abdomen absent (can be present on heavily marked specimens (Levy & Habeck 1976)). Segment 1 with lateral dark spot absent. Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle present. Spiracle with black border and pale center; not stalked. Subspiracular stripe inconspicuous, concolorous below spiracular band. Crochets uniordinal; total number on one side of body less than 106 (range: 77–88; mean: 84.5; n=10).

Color description.—Mature larvae range from 25–30 mm in overall body length. Head pale, with broad submedian arcs, reticulation, and a solid area posterior to ocelli fuscous or black. Pronotal shield infuscated. Ground color varies from green to soft shades of gray and brown to pinkish brown. Middorsal stripe pale, nearly absent on anterior and posterior portions of each abdominal segment by more intense fuscous markings anteriorly. Segmental spots black when present. Lateral band darker than dorsum. Lateral stripe white. Spiracular band a shade of lavender to black. Spiracles pale yellowish with dark rims. Venter green flecked with white (Swezey 1906; Fletcher 1914; Crumb 1927, 1956).

Plant hosts.—*S. exigua* is an important economic pest throughout the world. Hosts include many crops in the Fabaceae (peanuts, peas, beans, soybeans, lentils, alfalfa) and Poaceae (corn, millet, oats, wheat, rice, sorghum). Larvae also feed on a variety of horticultural crops including many species of cut flowers.

Discussion.—Considerable variation is found



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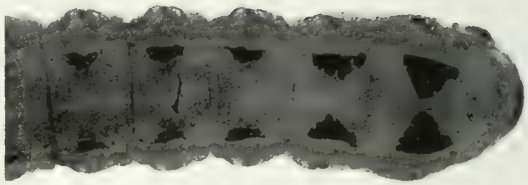

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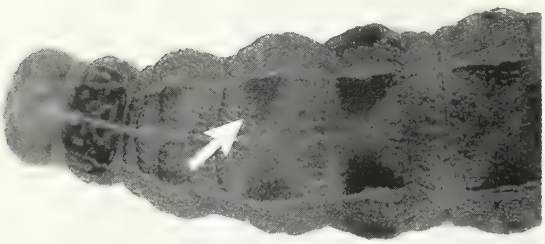

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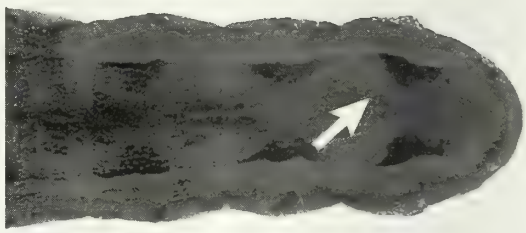

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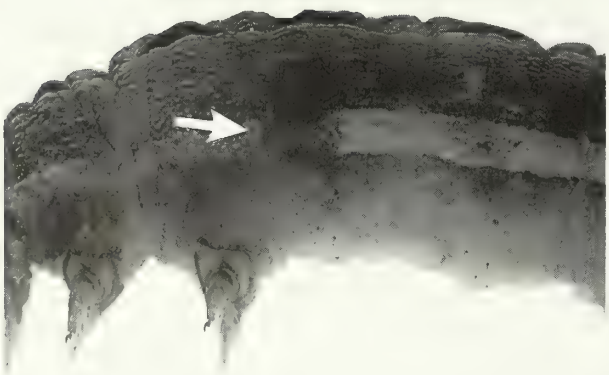

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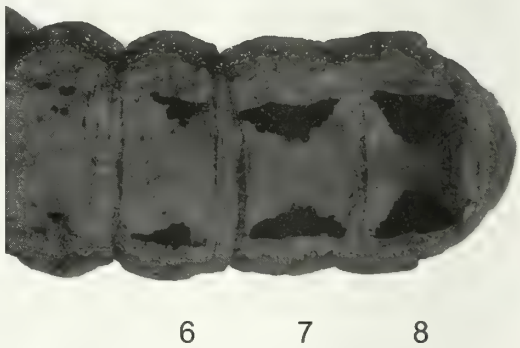

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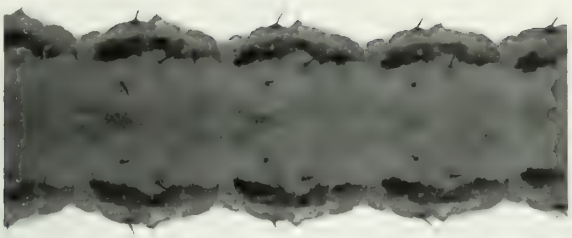
Figs. 144–149. *Spodoptera* larval key characters. 144, *S. albula,* dorsal view. 145, *S. dolichos,* dorsal view, numbers refer to abdominal segments 6–8. 146, *S. eridania,* dorsal view, arrow indicating spot on abdominal segment 1. 147, *S. eridania,* dorsal view, arrow indicating spot on abdominal segment 8. 148, *S. eridania,* lateral view, arrow indicating spiracular band interrupted by spot on abdominal segment 1. 149, *S. androgea,* lateral view, numbers refer to abdominal segments 6–8.



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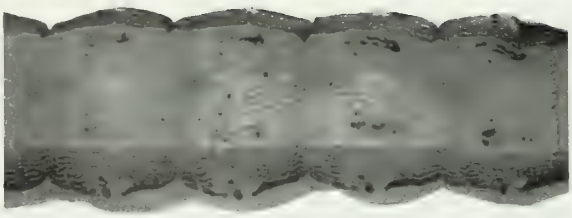

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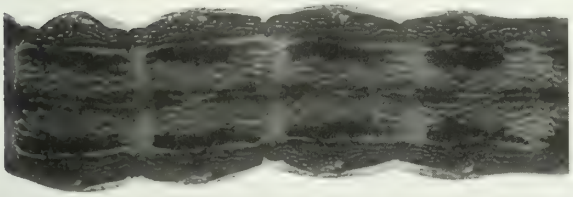

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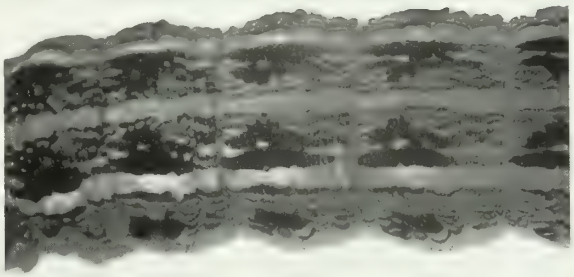

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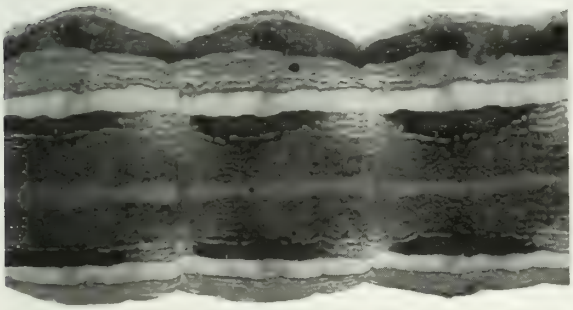

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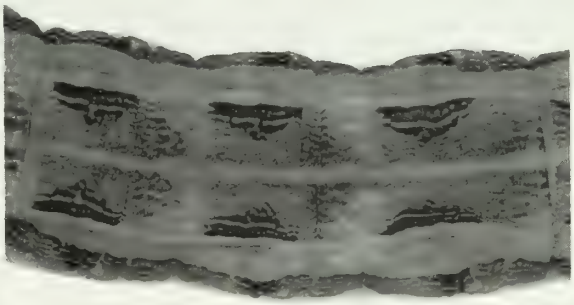

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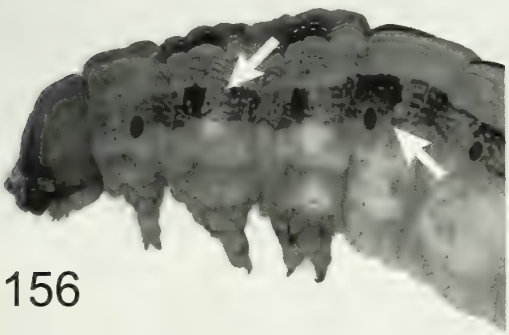

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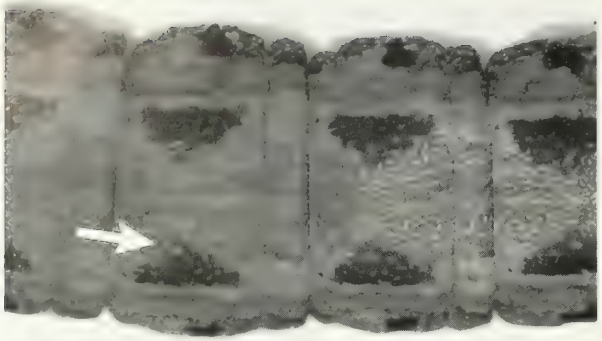
Figs. 150–157. *Spodoptera* larval key characters. 150, *S. frugiperda,* dorsal view. 151, *S. exigua,* dorsal view. 152, *S. exigua,* dorsal view of dark form. 153, *S. albula,* dorsal view. 154, *S. ornithogalli,* dorsal view. 155, *S. praefica,* dorsal view. 156, *S. praefica,* lateral view. 157, *S. ornithogalli,* lateral view.



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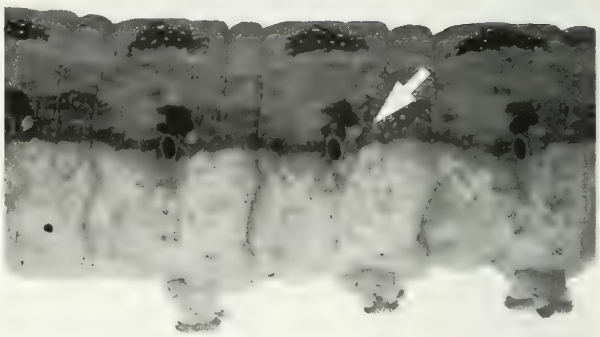

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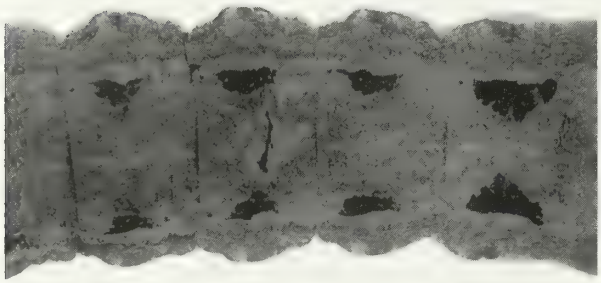

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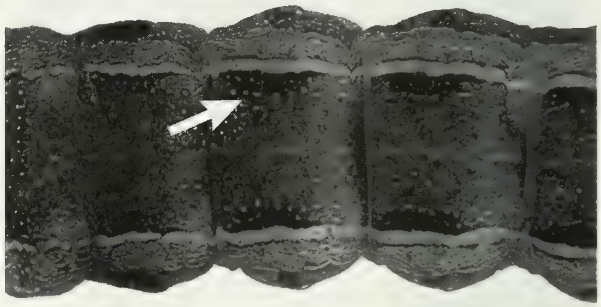

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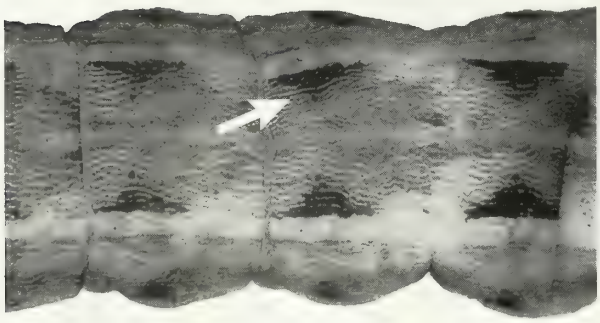

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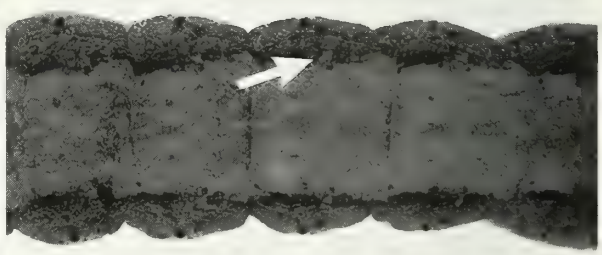

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Figs. 158–163. *Spodoptera* I key characters. 158, *S. Litura,* dorsal view. 159, *S. Litura,* lateral view. 160, *S. dolichos,* dorsal view. 161, *S. latifascia,* dorsal view. 162, *S. pulchella,* dorsal view. 163. *S. littoralis,* dorsal view.

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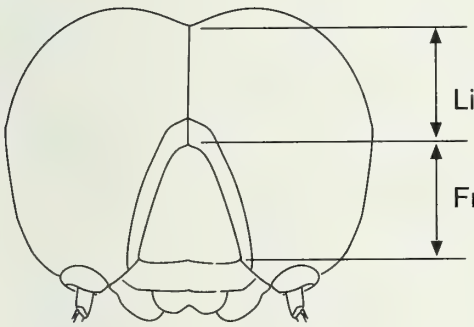

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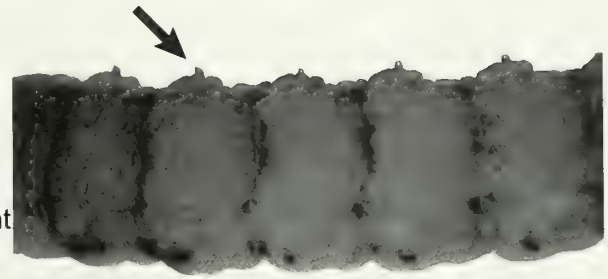

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Figs. 164–169. *Spodoptera* l key characters. 164, *S. latifascia,* lateral view. 165, *S. descoinsi,* lateral view. 166, ratio of edcysial line:frons height. 167, *S. pectinicornis,* dorsal view, arrow pointing to stalked spiracle. 168, *S. frugiperda,* left mandible. 169, *S. mauritia,* right mandible.

in the larva of *S. exigua*. Brown & Dewhurst (1975) reported that the ground color of individuals, all reared from the same brood under similar conditions were yellow, green, or brown, and with a shade of either pale, medium, or dark, with the darker ones being green. The head was brown and concolorous with the epicranial plates. Crumb (1956) described the ground color as ranging from green through shades of gray to brown and the head pale with submedian arcs and reticulation. In Honduras, most specimens were green with the head color green to black (Passoa 1991). In Hawaii larvae can be black to green, the black specimens have the middorsal and dorsolateral stripes yellowish; as the larva matures the ground color becomes more green with greenish stripes (Swezey 1906).

Spodoptera cilium Guenée

Diagnosis.—*S. cilium* larva can be confused with *S. exempta* and *S. mauritia* in Africa. *Spodoptera cilium* and *S. exempta* have a dark head, while *S. mauritia* has a light colored head. *Spodoptera exempta* has a solid spiracular line with distinct white spots caudad to spiracle; this is lacking in the other species. The white spots sometimes can be present in *S. cilium*, but they are never distinct. The dorsal abdominal markings are reduced to absent in *S. exempta*, are narrow in *S. mauritia*, and variable in *S. cilium*. These markings can be large and semicircular, reduced as in *S. mauritia*, or they may be of a characteristic crescent shape which is apparently peculiar to *S. cilium* (Brown & Dewhurst 1975).

Description.—*Head:* Cutting edge of mandible chisel-like, teeth not distinct; P2 setae closer together than P1 setae. *Thorax:* Pronotum with middorsal and dorsolateral stripes conspicuous. Segmental spots variable, can be semicircular, crescent-shaped, reduced and irregular, or absent. *Abdomen:* Body smooth; setal pinacula minute. Segmental spots variable, semicircular, narrow, or crescent-shaped (Brown & Dewhurst 1975).

Color description.—Head dark olive brown; adfrontal and coronal sutures pale; frons pale olive brown. Ground color pale drab. Middorsal stripe pale. Dorsolateral band brownish gray or darker pinkish brown. Segmental spots black. Dorsolateral stripe pale. Lateral band pale brown, brownish green or green. Spiracular band brown to dark purplish brown. Spiracular stripe purplish. Subspiracular stripe pale purplish. Spiracles black. Venter greenish. Thoracic legs greenish. Prolegs greenish (Sevastopulo 1941; Brown & Dewhurst 1975).

Plant hosts.—Nine species of hosts are recorded, most of which are grasses. *Spodoptera cilium* is a pest of turf and pasture grasses in Africa (Brown & Dewhurst 1975) and of rice in Pakistan (Ahmad & Kamaluddin 1991).

Discussion.—Sevastopulo (1941) gave a more complete description of the egg, larval instars, and pupa. Brown & Dewhurst (1975) discussed differences between *S. cilium* and other African *Spodoptera*. Larval damage is mainly to that of turf grasses and appears similar to damage reported for *S. mauritia* (Tanada & Beardsley 1958; Brown & Dewhurst 1975).

Spodoptera pecten Guenée

Diagnosis.—Similar to *S. mauritia* but is slightly smaller (Sevastopulo 1941).

Color description.—Head olive brown; adfrontal and coronal sutures whitish; frons honey colored. Prothoracic shield with middorsal and dorsolateral stripes pale. Ground color pale brownish gray or greenish gray. Middorsal stripe pale. Segmental spots black, lunule-shaped. Dorsolateral stripe pale. Lateral stripe purple. Spiracular stripe pale. Spiracles black. Venter greenish gray. Thoracic legs pale brown. Prolegs greenish gray (Sevastopulo 1941).

Plant hosts.—*S. pecten* is a pest of corn in Malaysia (Yunas & Hua 1980) and of rice in Malaysia (Dammerman 1929), India (Chatterjee 1969), and China (Wu 1982). Hosts are not restricted to grasses, since the species has been reared from Brassicaceae (radishes), Euphorbiaceae (*Aleurites montana* Wilson), Fabaceae (*Derris elliptica* Benth.), and Malvaceae (*Hibiscus rosa-sinensis* L.) (Yunas & Hua 1980). Ten different host plants have been recorded.

Discussion.—No larvae were available for study. For a more complete description including egg, and early instar, half grown, penultimate, and last instar larvae see Sevastopulo (1941).

Spodoptera pectinicornis (Hampson)

Figs. 167, 474–476

Diagnosis.—This is the most distinctive of all *Spodoptera* larvae. Its spiracles are stalked (Fig. 167) and the crochets are biordinal. There are no dorsal abdominal markings typically found in most other species.

Description of preserved specimens.—*Head:* Color brown; reticulate; frons yellowish brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe in form of a large spot; middorsal stripe narrow. Mesothorax segmental spot absent; with lateral dark spot absent. Metathorax with segmental spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe absent. Segmental spots on abdomen absent. Segment 1 with lateral dark spot absent. Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band solid; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle absent. Spiracles with black border and pale center; stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets biordinal; total number on one side of body greater than 107 (total number: 133; n=1)

Host plants.—This species is monophagous and feeds only on waterlettuce, *Pistia stratiotes* (L.) (Araceae). It was released in 1990 in Florida as a biological control agent but has so far not become established (Habeck & Thompson 1994).

Discussion.—Only one specimen was available for study. The stalked spiracles may be due to the semi-aquatic environment of the larvae.

Spodoptera eridania (Stoll)

Figs. 146–148, 477–479

Diagnosis.—The subspiracular line is either interrupted or loses intensity at the lateral spot. The black dorsal triangles on the first abdominal segment are large and equal in size to those on the eighth segment. The total number of crochets on one side of body ranges from 97–109 with an average of 102.9. The number of crochets is important as only *S. exigua* and *S. frugiperda* share this character. *Spodoptera eridania* can be easily separated from *S. frugiperda* by the lack of large, conspicuous, dorsal pinacula. *Spodoptera exigua* is much smaller and usually lacks dorsal triangular markings on the abdomen. If they are present, then they are smaller and do not reach near the middorsal line.

Description of preserved specimens.—*Head:* Color yellowish brown; reticulate; frons yellowish brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe wider than dorsolateral stripe. Mesothorax segmental spot rectangular (can be inconspicuous); with lateral dark spot absent. Metathorax with segmental spot triangular; white spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots equal in size on abdominal segments 1 and 8, smaller on 2–6; wide on segments 1 and 8, almost extending to middorsal stripe; lacking contrasting marks; on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present (can be smaller and not enclosing spiracle). Segments 2–6 with lateral dark spots in spiracular band absent (can be small and obscure when spiracular band mottled). Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle present (can be inconspicuous). Spiracles with black border and brown center; not stalked. Subspiracular stripe interrupted on abdominal segment 1, inconspicuous beyond segment 1. Crochets uniordinal; total number on one side of body averages less than 106, but some specimens can have as many as 109 (range: 97–109; mean: 102.9; n=10).

Color description.—Mature larvae 35–38 mm in length. Head ground color yellow heavily suffused with bright reddish-brown reticulation which is more or less fused forming solid areas of reddish brown; adfrontal sutures pale but not white; adfrontal area brown. General dorsal color a deep, uniform gray sometimes tinged with olivaceous or pinkish. Middorsal stripe, dorsolateral stripe, and subspiracular stripe unicolorous, whitish tinged with orange or pinkish. Segmental spots a series of black triangles angulate on their dorsal faces. Lateral band dark fuscous, dorsal half paler. Venter pale, suffused with pinkish or orange and much flecked with white. Spiracles brown with dark rims. Thoracic legs uniform infuscated brown. Prolegs pinkish (Crumb 1929, 1932).

Plant hosts.—*S. eridania* is polyphagous with 102 species of larval hosts recorded. Important agricultural crops on which it feeds include corn, tomatoes, potatoes, beans, and sweet potatoes. Scriber (1986) hypothesized that pokeweed may be a natural host plant of *S. eridania*. He observed

4 separate groups of larvae feeding on pokeweed (*Phytolacca rigida* (Small), Phytolaccaceae) among many other species of potential hosts. Only the pokeweed was utilized as a host. Since *S. eridania* is among one of the most polyphagous species of *Spodoptera,* were the larvae showing some type of preference for pokeweed?

Discussion.—The ground color is uniformly gray tinged with olivaceous or pinkish (Crumb 1929, 1956). The ground color recorded by Passoa (1991) is a dark grayish green. Dorsal triangular markings can be present on all segments except the prothorax, but they can be reduced to narrow lines or absent on abdominal segments 2–6. They are usually largest on abdominal segments 1 and 8. Head ground color is a pale yellow overlaid with bright reddish brown reticulation which form solid areas of reddish brown (Crumb 1929, 1956). See Crumb (1929, 1956) for a more detailed description of the larva. Keys that include *S. eridania* are found in Levy & Habeck (1976) and Passoa (1991).

Spodoptera albula (Walker)

Figs. 144, 153, 480–482

Diagnosis.—The only reliable character to identify the larva of *S. albula* is the presence of a white spot near the apex of the dorsal triangular markings of the meso- and metathorax and abdomen (Fig. 153).

Description of preserved specimens.—*Head:* Color yellowish brown; reticulate; frons yellowish brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe absent or inconspicuous, consisting of only a few faded spots at margins; middorsal stripe narrower than dorsolateral stripe. Mesothorax segmental spot triangular; with lateral dark spot absent. Metathorax with segmental spot triangular; white spot at apex of segmental spot; lateral dark spot present (can be absent). *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe large, subequal to dorsolateral stripe. Segmental spots uniform in size on abdominal segments 1–8; wide on segments 1–6, almost extending to middorsal stripe; with a distinct white spot near apex of each segmental spot; on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present. Segments 2–6 with lateral dark spots in spiracular band present. Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle present. Spiracles with black border and pale center; not stalked. Subspiracular stripe inconspicuous, concolorous below spiracular band. Crochets uniordinal; total number greater than 107.

Color description.—Head brownish; front brown containing dorsal and ventral pair of mediolateral black spots just inside brown to black epicranial arms; clypeus uniformly brown; adfrontal area yellowish brown; reticulation yellowish; submedian arcs black, small, variously shaped; area laterad to arcs yellowish brown; setae, papillae, punctures brown; pinacula yellow. Ground color of body gray to yellowish brown to blackish. Middorsal stripe yellowish brown, often centrally streaked with brown or black. Dorsolateral band variable, gray, brown, or black, often flecked and streaked whitish gray. Segmental spots triangular, black, occasionally with minute white flecks, each triangular spot possessing a distinct white apical spot or notch. Anal and cervical shields grayish brown and freckled white or yellow. Lateral band usually indistinct, entire area densely streaked and flecked white on a gray ground, a narrow, slightly paler dorsal area occasionally visible. Subspiracular stripe pale, densely flecked whitish gray on brown ground with distinct, narrow, yellow line separating it from spiracular band. Thoracic legs grayish brown. Prolegs tan, shields black (Levy & Habeck 1976).

Plant hosts.—Only thirteen hosts are recorded, but several agricultural crops are included: cabbage, peanuts, soybean, cotton, corn, tomato, and tobacco.

Discussion.—Passoa (1991) illustrated two color forming of the larva, one with reduced dorsal triangles where the white spots are circled with a thin black line and the other a variegated color form where the white spots are more difficult to distinguish among the smaller white spots. Keys that include *S. albula* are found in Levy & Habeck (1976) and Passoa (1991).

Spodoptera exempta (Walker)

Figs. 483–485

Diagnosis.—In *S. exempta* the spiracular band is solid in color with a white spot caudal to the spiracle. The head and frons are dark brown. The dorsal thoracic and abdominal markings are usually absent or greatly reduced. *Spodoptera exempta* could be confused with *S. mauritia* and *S. cilium,*

but neither have a solid spiracular band and both usually have dorsal thoracic and abdominal markings, though they can be quite reduced. Some specimens of *S. cilium* can have a white spot caudal to the spiracle, but it is not as prominent as in *S. exempta* (Brown & Dewhurst 1975).

Description of preserved specimens.—*Head:* Color brown; reticulate; frons dark brown; cutting edge of mandible chisel-like teeth not distinct; P2 setae closer together than P1 setae; ratio ecdysial line: frons height, averages greater than 0.88. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax segmental spot absent; with lateral dark spot absent. Metathorax with segmental spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe large, subequal to dorsolateral stripe. Segmental spots on abdomen absent. Segment 1 with lateral dark spot absent. Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band solid; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle present. Spiracles with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107 (range: 116–134, average: 123; n=5).

Color description.—Ground color grass green to black. Middorsal stripe white. Dorsolateral stripe white. In black form, dorsolateral stripe and spiracular band darker than other stripes; subspiracular stripe yellowish (sometimes pinkish). Spiracles black. Venter pale (Swezey 1909).

Plant hosts.—Brown (1962) listed 36 species of Poaceae and four of Cyperaceae as hosts of *S. exempta* in East Africa. A few other species of grasses have been added since (Brown & Dewhurst 1975). *Spodoptera exempta* is predominantly a grass feeder attacking corn, rice, millet, sorghum, wheat, sugar cane, and pasture grasses. It is rare on dicotyledons and probably eats these plants when species of Poaceae and Cyperaceae are absent.

Discussion.—Preserved larvae in the USNM collection show two distinct color morphs, a dark form and light form. Experiments were conducted by Faure (1943) and Matthee (1946) on phase polymorphism in *S. exempta.* Faure (1943) attempted to group larvae reared in crowds and isolation into three categories based on color ranging from dark ("gregaria"), to medium ("transiens"), to light ("solitaria"). Phase coloration could be manipulated by rearing larvae in crowds and in isolation. The larvae reared in crowds were the dark, *gregaria* form. Larvae reared in isolation showed all three forming with less than 2% being *gregaria,* 32–48% *transiens,* and 57–68% *solitaria.* Development took six instars when larvae were reared in crowds and 88.4% took five instars when larvae were reared in isolation (Matthee 1946).

Spodoptera mauritia (Boisduval)

Figs. 169, 464–470, 486–488

Diagnosis.—The best character to separate *S. mauritia* from *S. exempta* is the reticulate spiracular band which lacks white or light colored spots caudad to the spiracles. *Spodoptera exempta* has a solid band with well defined spots caudad to the spiracles. The frons is yellowish brown contrasting to the brown head; in *S. exempta* the frons is dark brown and concolorous with the head. *Spodoptera triturata* has larger and more distinct dorsal abdominal markings that are more triangular in shape.

Description of preserved specimens.—*Head:* Color brown; reticulate; frons yellowish brown; cutting edge of mandible chisel-like, teeth not distinct; P2 setae closer together than P1 setae; ratio ecdysial line: frons height, averages greater than 0.88. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax segmental spot elongate, narrow rectangle; with lateral dark spot present (small, can be faint). Metathorax with segmental spot an elongate, narrow rectangle; white spot absent; lateral dark spot present (small, can be absent). *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe large, subequal to dorsolateral stripe. Segmental spots uniform in size on abdominal segments 1–8; narrow on segments 1–6, extending no more than half the distance between dorsolateral and middorsal stripe; lacking contrasting marks; spot on 8th abdominal segment subequal in size to that on mesothorax. Segment 1 with lateral dark spot present. Segments 2–6 with lateral dark spots in spiracular band present. Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle absent. Spiracles with black border and brown center; not

stalked. Subspiracular stripe inconspicuous, concolorous below spiracular band. Crochets uniordinal; total number on one side of body less than 106 (range: 83–97; average: 90.4; n=10).

Color description.—Head brown to olive brown, darkest in a band laterad of the adfrontal and coronal sutures; frons testaceous to sordid whitish; adfrontal and coronal sutures pale; regions of ocelli and genae are irregularly testaceous. Pronotal shield brownish with 3 narrow pale yellow or white stripes. Ground color dark gray to dark green. Middorsal stripe faint, irregular, darker than dorsolateral stripe, purplish. Dorsolateral band predominantly grayish, varying in shade among different individuals. Segmental spots black. Dorsolateral stripe almost pure pale yellow to light reddish brown. Lateral band grayish with a yellow or greenish tinge. Lateral stripe often interrupted, pale. Spiracular band darker than lateral band, purplish brown to reddish. Subspiracular band pale yellowish to light reddish brown. Spiracles black, brownish internally. Venter greenish. Thoracic legs testaceous. Prolegs pale. (Fletcher 1914; Sevastopulo 1939a; Gardner 1941; Tanada & Beardsley (1958).

Plant hosts.—*S. mauritia* is predominantly a feeder on Poaceae and Cyperaceae. Over 40 plant hosts were found in the literature. The agriculturally important species known to be hosts include rice, millet, sugarcane, corn, sorghum, and pasture grasses. More information on host plant preferences is found in Tanada & Beardsley (1958) and Rothschild (1969). Again, caution must be used when literature citations refer to dicotyledons. Tanada & Beardsley (1958) reported no survival on tomato and tobacco (Solanaceae), but there are old records in the literature for tobacco from Mauritius (Corbett 1926).

Discussion.—Variation occurs in the overall coloration with light and dark forms. Body pattern seems to be fairly constant. Sevastopulo (1939a) described the larva from India. Brown & Dewhurst (1975) included *S. mauritia* in a key to larvae and gave a brief account of it from Africa.

Spodoptera triturata (Walker)

Diagnosis.—This species has the dorsolateral abdominal markings larger and more triangular shaped than in *S. mauritia* (Brown & Dewhurst 1975).

Description.—*Head:* Color brownish; cutting edge of mandible chisel-like, teeth not distinct; P2 setae closer together than P1 setae. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe large, subequal to dorsolateral stripe. Segmental spots lacking contrasting marks; spot on 8th abdominal segment larger than on mesothorax; spots large on segments 1–6, almost extending to middorsal stripe; uniform in size from abdominal segments 1–8. Subspiracular stripe continuous through abdominal segment 1 (Brown & Dewhurst 1975).

Plant hosts.—Little is known about the plant hosts of *S. triturata.* It appears to be a grass feeder. Dick (1943) reported the species feeding on sugarcane in Natal. Descamps (1956) listed it as feeding on rice in Cameroon. In the laboratory, it can be reared on grass (e.g., *Cynodon dactylon*), and, even though it can be reared on corn, it has never been found on corn in the field (Brown & Dewhurst 1975).

Discussion.—No specimens were available for study. Brown & Dewhurst (1975) provided a key that includes the African species, including illustrations of the larvae. *Spodoptera triturata* is not a pest and larvae are infrequently encountered.

Spodoptera frugiperda (J.E. Smith)

Figs. 150, 168, 489–491

Diagnosis.—Two characters that will separate *S. frugiperda* from other *Spodoptera* are the large pinacula and the granulose texture of the skin. No other *Spodoptera* has this combination of characters.

Description of preserved specimens.—*Head:* Color brown; reticulate; frons yellowish brown; cutting edge of mandible serrate; P2 setae closer together than P1 setae; ratio ecdysial line: frons height, averages greater than 0.88. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe subequal to dorsolateral stripe. Mesothorax segmental spot absent; with lateral dark spot absent. Metathorax with segmental spot absent; lateral dark spot absent. *Abdomen:* Body with pavement granules; setal pinacula large. Middorsal stripe large, subequal to dorsolateral stripe. Segmental spots on abdomen absent. Segment 1 with lateral dark spot present (can be absent). Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle absent. Spiracle with black border and brown cen-

ter; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body equal to or less than 106 (range: 85–106; average: 92.6; n=10).

Color description.—Mature larvae about 30 mm in length; width of head capsule 2.6 - 2.8 mm. Head grayish, pale yellowish, or brownish; adfrontal areas and adjacent margin of the head shield white; submedian arcs slender, reticulation close, ferruginous or brownish. Ground color varying from pinkish, through yellowish, olivaceous, and dull gray to almost black. Middorsal stripe yellowish. Dorsolateral band of ground color overlaid with strands and flecks of brownish and fuscous. Dorsolateral stripe yellowish. Lateral band to spiracular band infuscated, intensified on its dorsal margin to form black dashes on anterior half of each abdominal segment. Subspiracular band yellow or whitish mottled with ferruginous. Spiracles pale with black rims and margined with whitish (Crumb 1927, 1956).

Plant hosts.—This is an extremely polyphagous species with 98 species of host plants in 27 families recorded in the literature. The fall armyworm is most injurious to corn and rice. Other important agricultural crops it attacks include cabbage, beet, peanut, soybean, alfalfa, onion, cotton, pasture grasses, millet, sugarcane, sorghum, tomato, potato.

Discussion.—The head color varies from almost completely pale yellowish brown to mostly brown. The reticulation is lighter than the head with a pale area surrounding stemmata. Various shades of ground color are evident in preserved specimens. Illustrations of all life stages are found in Valverde, *et al.* (1995).

Spodoptera dolichos (Fabricius)

Figs. 145, 160, 492–494

Diagnosis.—The differences between *S. dolichos* and *S. androgea* are discussed under the latter. In North America *S. dolichos* could be confused with *S. latifascia*. The best character to distinguish these species is the dorsal markings of the metathorax. *Spodoptera dolichos* has large, trapezoidal markings and *S. latifascia* has smaller, semicircular markings. These dorsal markings are similar in size on the metathorax and the eighth abdominal segment in *S. dolichos*, but the metathoracic markings are smaller than those on the eighth abdominal segment in *S. latifascia*.

Description of preserved specimens.—*Head:* Color brown; reticulate; frons brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe absent or inconspicuous, consisting of only a few faded spots at margins; middorsal stripe wider than dorsolateral stripe. Mesothorax segmental spot trapezoidal; with lateral dark spot absent. Metathorax with segmental spot round; white spot at base of segmental spot; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots on abdominal segments 7 and 8 larger than on 1–6; narrow on segments 1–6, extending no more than half the distance between dorsolateral and middorsal stripe and large on segments 7 and 8, almost extending to middorsal stripe; spots lacking contrasting marks; spot on 8th abdominal segment subequal in size to that on mesothorax. Segment 1 with lateral dark spot absent (present in 4th and earlier instars). Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band reticulate; segments 1–6 in spiracular band with white or light colored spot caudal to spiracle absent. Spiracles with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107 (range: 109–156; average: 134.1; n=10).

Color description.—Head brown, fuscous dorsally and with yellowish flecks posteriorly; adfrontal sutures yellowish white and terminating distinctly before reaching occipital foramen. General ground color ocher yellow tinged with glaucous and overlaid to a varying degree with fuscous flecks so general dorsal color varies from very light to very dark gray, usually light gray. Middorsal stripe orange. Dorsolateral band orange, yellow above. Segmental spots indistinct diamond-shaped, fuscous, connected at their lateral angles with a series of jet black spots, linear anteriorly, larger and more triangular posteriorly. Lateral band of dorsal color, darker below. Lateral stripe a broken yellow line. Subspiracular stripe orange, sinuate, with a similar band of white flecks below. Venter dull brownish closely flecked with clear white. Thoracic legs brown, fuscous apically. Prolegs brownish, tinged with pink, shields brownish (Crumb 1929).

Plant hosts.—Seventeen species of plants are recorded as hosts for *S. dolichos.* Many families are reported, but Solanaceae is the most common with larvae feeding on tomatoes, potatoes, and tobacco. Other crops that have been recorded as hosts include turnips, cotton, sweet potatoes, and asparagus.

Discussion.—There is variation in frequency and intensity of the dorsal markings, with some specimens bearing these marks on the mesothorax to the eighth abdominal segment. Other specimens are only marked on the mesothorax and seventh and eighth abdominal segments. The lateral spot near the spiracle on the first abdominal segment can be present or absent.

Crumb (1929) described all six instars and gave some life history data. Passoa (1991) illustrated the larva in color.

Spodoptera androgea (Stoll)

Figs. 149, 495–497

Diagnosis.—*S. androgea* is most likely to be confused with *S. dolichos.* The dorsal markings on the metathorax and eighth abdominal segment are smaller than in *S. dolichos.* The dorsal markings of the eighth abdominal segment can be contiguous or near the middorsal line in *S. dolichos,* in *S. androgea* these markings are smaller and never contiguous or near the middorsal line. Dorsal markings on the metathorax are not present in *S. androgea* but can be present or absent in *S. dolichos.* The bases of prolegs 3–6 are darker in *S. androgea.*

Description of preserved specimens.—*Head:* Color brown; not reticulate; frons dark brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax segmental spot trapezoidal; with lateral dark spot absent. Metathorax with segmental spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots on abdominal segments 7 and 8 larger than on 1–6; narrow on segments 1–6, extending no more than half the distance between dorsolateral and middorsal stripe; spots with narrow white dashes; spot on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present. Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band reticulate; segments 1–6 in spiracular band with white or light colored spot caudal to spiracle present. Spiracle with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107.

Color description.—Known only from preserved specimens.

Plant hosts.—Only one literature record reports this from Brazil on cacao (Zucchi & Silveira Neto 1984). It was reared on *Xanthosoma* sp. (Araceae) by B. Marquis (Passoa pers. comm.) in Costa Rica, and it was reared in the laboratory on *Amaranthus* sp. (Amaranthaceae) in Guadeloupe (www.jouy.inra.fr/papillon/noctuid/amphipyr/texteng/s_androg.html).

Discussion.—Five specimens preserved in alcohol were examined. Eggs were obtained from a female originating from French Guiana, and the larvae were fed artificial diet. Based on head width measurements, two specimens were fifth instar (head width 2.40–2.50 mm) and three sixth instar (head width 3.55–3.65 mm). Specimens in the fifth instar were lighter with the dorsolateral stripes of the pronotum present. The rectangular dorsolateral mark on the mesothorax can vary in size and shape by becoming more elongate.

Spodoptera littoralis (Boisduval)

Figs. 163, 498–500

Diagnosis.—Characters useful for identification include the serrate edge of the mandible, P2 setae farther apart than P1 setae, absence of dorsolateral stripe on the pronotum, and metathorax with a dorsolateral mark. This species could be confused with *S. exigua,* especially in the early instars, but in *S. exigua* the dorsolateral stripe is present on the pronotum and the metathorax lacks dorsolateral spots. Larvae of *S. littoralis* are either light or dark brown, in *S. exigua* they can be brown or green (Brown & Dewhurst 1975). *Spodoptera littoralis* is larger than *S. exigua. Spodoptera litura* can be distinguished from *S. littoralis* by the prominent lateral spots present from the mesothorax to the eighth abdominal segment.

Description of preserved specimens.—*Head:* Color brown; reticulate; frons brown; cutting

edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe absent or inconspicuous, consisting of only a few faded spots at margins; middorsal stripe narrower than dorsolateral stripe. Mesothorax segmental spot rectangular to semicircular; with lateral dark spot present (indistinct). Metathorax with segmental spot round; white spot at base of segmental spot; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots on abdominal segments 7 and 8 larger than on 1–6; wide on segments 1 and 8, almost extending to middorsal stripe; a white spot mid-basally in segmental spot (segmental spots can be reduced to a dark line, but spot is still present); on 8th abdominal segment spot is subequal in size to that on mesothorax. Segment 1 with lateral dark spot absent. Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band reticulate; segments 1–6 in spiracular band with white or light colored spot caudal to spiracle present (indistinct). Spiracles with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107.

Color description.—Head black; adfrontal and coronal sutures yellow. Ground color purplish black. Segmental triangular spots black. Venter pale. Thoracic legs black (Sevastopulo 1939a).

Plant hosts.—*S. littoralis* is a polyphagous species recorded from 130 species in 56 families of host plants. It is one of the most agriculturally important species over its range. Many plants it attacks are of major economic importance such as taro, cabbage, beet, castor oil plant, peanut, soybean, green gram, rice, cotton, corn, tomato, and tobacco.

Discussion.—Overall color variation was present in specimens and included several shades of brown. The dorsolateral mark on the mesothorax can vary from an irregularly shaped rectangle to an almost round spot. The same mark on the metathorax can also vary from an irregular to a round spot. Sympatry of *S. littoralis* and *S. litura* in western Asia is still not certain, so close examination of larvae from this area is warranted for a correct identification.

***Spodoptera litura* (Fabricius)**

Figs. 158–159, 501–503

Diagnosis.—*Spodoptera litura* can be differentiated from *S. mauritia* by the serrate edge of the mandible in *S. litura*. This species can be separated from *S. exigua* because *S. litura* has dorsolateral marks on the meso- and metathorax, a smaller number of crochets on the prolegs, and the ratio of the ecdysial line versus frons height averages between 0.63–0.84.

Description of preserved specimens.—*Head:* Color brown; reticulate; frons brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe subequal to dorsolateral stripe. Mesothorax segmental spot semicircular to rectangular; with lateral dark spot present. Metathorax with segmental spot semicircular; white spot at base of segmental spot; lateral dark spot present. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots on abdominal segments 7 and 8 larger than on 1–6 (variable, can be almost uniform in size on some specimens); wide on segments 1–6, almost extending to middorsal stripe (can be faint); with a distinct white spot near apex; spot on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present. Segments 2–6 with lateral dark spots in spiracular band present. Spiracular band reticulate; segments 1–6 in spiracular band with white or light colored spot caudal to spiracle present. Spiracles with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107 (range: 116–141; average: 127.3; n=10).

Color description.—Head dark brown to black, pale brown on vertex and with pale marks laterally; frons dark brown to black; adfrons white. Pronotal shield black with pale speckling. Ground color dark grayish to blackish with pale speckling. Middorsal stripe yellow. Segmental spots black. Dorsolateral stripe yellow. Subspiracular stripe dull yellow. Spiracles black. Venter dull green. Thoracic legs black. Proleg shields black (Fletcher 1914; Gardner 1941).

Plant hosts.—*Spodoptera litura* is the most polyphagous species of *Spodoptera* with 151 species in 51 families of recorded host plants. Like *S. littoralis*, this species is not confined to a few families, and both have similar hosts plants. Agriculturally important crops attacked include cotton, rice, green gram, corn, cabbage, beet, peanut, soybean, castor oil plant, tomato, and tobacco.

Discussion.—Variation occurs in the ground color with both light and dark forms known. Ground color variation influences head color, which varies from yellowish brown to dark brown. Dorsolateral abdominal marks can be prominent or greatly reduced to absent, especially on segments 2–6.

Color illustrations and descriptions of all life stages were given by Fletcher (1914, plate XIX). Larval descriptions are found in Gardner (1941) and Mochida (1973). Cayrol (1972) described the larva and discusses the biology and economic importance of this species.

Spodoptera picta (Guérin-Méneville)

Figs. 504–506

Diagnosis.—This is a distinct larva with a wide yellow middorsal stripe. It also has large segmental spots on abdominal segment 1, small black lunules on segments 2–6, larger lunules on segment 7, and spots on segment 8 similar in size to those on segment 1.

Description of preserved specimens.—*Head:* Color yellowish brown; faintly reticulate; frons yellowish brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages greater than 0.88. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe wider than dorsolateral stripe. Mesothorax segmental spot absent; with lateral dark spot absent. Metathorax with segmental spot absent; white spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe large, subequal to dorsolateral stripe. Segmental spots equal in size on abdominal segments 1 and 8, smaller on 2–6; wide on segments 1 and 8, narrow on 2–6, located just above dorsolateral stripe; lacking contrasting marks; spot on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present. Segments 2–6 with lateral dark spots in spiracular band present. Spiracular band reticulate; segments 1–6 in spiracular band without white or light colored spot caudal to spiracle. Spiracles with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107 (range: 150–174; average: 162; n=2).

Color description.—Head brown. Pronotal shield black, with middorsal stripe yellow, dorsolateral stripe white. Ground color gray. Middorsal stripe wide, yellow. Dorsolateral band with white streak. Dorsolateral stripe white. Lateral band pale. Spiracular band dark (Sevastopulo 1939b, Gardner 1941).

Plant hosts.—The hosts of *S. picta* seem to be restricted to Liliaceae. Sevastopulo (1939b) listed Liliaceae as a host. Holloway (1979) refers to two hosts, *Crinum asiaticum* L. and *C. pedonculatum* R. Br., both in the Liliaceae. Crossley (1998) considered *S. picta* a minor pest of gardens in Australia, feeding on amaryllis (*Hippeastrum* sp., Liliaceae).

Discussion.—Color photographs of this species can be found on the Lepidoptera of Australia website (http: //linus.socs.uts.edu.au/~don/larvae/larvae.html). The larvae feed gregariously (Sevastopulo 1939b).

Spodoptera latifascia (Walker)

Figs. 161, 164, 507–509

Diagnosis.—The dark form of *S. latifascia* can be confused with the dark form of *S. ornithogalli*. In *S. ornithogalli* the white markings passing through the dorsal triangular markings are a series of fine white lines and dashes. These markings in *S. latifascia* are a series of white spots. The ratio between the ecdysial line and frons height can separate these species. This ratio in *S. latifascia* is less than 0.62, and is between 0.63 and 0.84 in *S. ornithogalli*.

Description of preserved specimens.—*Head:* Color yellowish brown; not reticulate; frons yellowish brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages less than 0.62. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax segmental spot semicircular; with lateral dark spot absent. Metathorax with segmental spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrow-

er than dorsolateral stripe. Segmental spots on abdominal segments 7 and 8 larger than on 1–6; narrow on segments 1–6, extending no more than half the distance between dorsolateral and middorsal stripe (can be absent); with a dotted line along anterior margin; on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present (can be absent). Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle absent. Spiracles with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107 (range: 122–144; average: 133; n=10).

Color description.—Mature larvae about 48 mm in length. Head yellowish brown; front brown containing dorsal and ventral pair of mediolateral white to yellow spots just inside epicranial arms, occasional dark mark occurring between ventral pale spot and dark brown epicranial arms; clypeus yellowish brown, ventral margin sometimes bordered dark brown; adfrontal area yellow; reticulation yellow to tan; submedian arcs brown; vertex brown; ocular area yellowish brown. Ground color grayish blue-green to dark reddish brown. Middorsal stripe obscure, faintly whitish pink on several abdominal segments. Dorsolateral band densely flecked with white, varying from gray to greenish blue to nearly black and often paler between segmental triangular spots. Segmental spots triangular to semicircular, black occasionally flecked with white. Anal and cervical shields grayish brown to black, flecked with white. Dorsolateral stripe white. Lateral band grayish blue to brown, sometimes containing 3 narrow pink or white streaked lines, occasionally densely flecked. Lateral stripe orange or yellow. Spiracular band grayish green or black with white flecking. Subspiracular stripe yellow to orange. Subspiracular band grayish brown to bluish green with diffuse white flecks. Venter gray to greenish blue to nearly black, densely flecked over prolegs and thoracic legs, between legs paler. Thoracic legs brown to black. Prolegs dark pink to brown, shields black (Levy & Habeck 1976).

Plant hosts.—Only eight host plants are recorded for *S. latifascia.* This species is of economic importance on lettuce and tomato in Costa Rica, corn and tomato in El Salvador (McGuire & Crandall 1967), and cotton in Barbados (Ingram 1978) and Honduras (Howell 1978).

Discussion.—Levy & Habeck (1976) first described the larva of *S. latifascia.* Passoa (1991) illustrated both the black and brown forming. Some specimens can lack the dorsal triangular markings on the abdomen.

Spodoptera descoinsi Lalanne-Cassou & Silvain

Figs. 165, 510–512

Diagnosis.—The head can be yellowish brown to dark brown with a dark brown frons. The dorsolateral markings of the mesothorax are semicircular, but very faint to almost absent. These markings are also very faint and small on abdominal segments 2–6, becoming larger and more distinct on segments 7 and 8.

Description of preserved specimens.—*Head:* Color yellowish brown to dark brown; reticulate; frons dark brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax segmental spot semicircular (very faint); with lateral dark spot absent. Metathorax with segmental spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots on abdominal segments 7 and 8 larger than on 1–6; narrow on segments 1–6, extending no more than half the distance between dorsolateral and middorsal stripe; with a dotted line along anterior margin; spot on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot absent. Segments 2–6 with lateral dark spots in spiracular band absent. Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle absent. Spiracles with black border and pale center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107.

Color description.—Known only from preserved specimens.

Plant hosts.—The only specimens available were those reared in the laboratory on a semi-artificial diet supplemented with cabbage and corn

powder (Monti *et al.* 1997). The hosts of *S. descoinsi* are probably similar to those of *S. latifascia.*

Discussion.—Only three larvae preserved in alcohol were available for study. Head color varies from a yellowish brown to dark brown. The frons is consistently dark brown. The dorsolateral marks of the abdomen are faint to absent on segments 2–6 and become larger on segments 7 and 8, though they are not as distinct as in other *Spodoptera* species.

Spodoptera praefica (Grote)

Figs. 155–156, 513–515

Diagnosis.—The larvae of this species most closely resemble those of *S. ornithogalli.* The middorsal stripe on the prothorax of *S. praefica* is almost as wide as the dorsolateral stripes; in *S. ornithogalli* the middorsal stripe is much narrower. The lateral spot on abdominal segment 1 is less than half the width of the segment, whereas in *S. ornithogalli* the lateral spot is more than half the segment width. The head of *S. ornithogalli* has more black and the frons is either all black or mostly black as compared to *S. praefica* which has a thin border of black on the frons and a small amount of black at the apex (pale form).

Description of preserved specimens.—*Head:* Color yellowish brown; reticulate; frons yellowish brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax with segmental spot triangular; with lateral dark spot present. Metathorax with segmental spot triangular; white spot absent; lateral dark spot present. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots uniform in size from abdominal segments 1–8; wide on segments 1–6, almost extending to middorsal stripe; each with a line passing through; on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present. Segments 2–6 with lateral dark spots in spiracular band present. Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle present. Spiracles with black border and pale center; not stalked. Subspiracular stripe inconspicuous, concolorous below spiracular band. Crochets uniordinal; total number on one side of body greater than 107 (range: 120–145; average: 129.5; n=10).

Color description.—Mature larva 20–46 mm in length. Head ground color brownish to brownish orange heavily reticulated with blackish or reddish markings; adfrontal sutures and areas yellowish white forming a conspicuous inverted V. Ground color variable from almost pure creamy white to black with yellow. Dorsolateral stripe yellow in black specimens. Spiracular band dark. Dark specimens with pale lateral and subspiracular stripes. (van den Bosch & Smith 1955).

Plant hosts.—This species has been recorded from 43 species of plant hosts in 16 families. Agriculturally important plants it attacks include alfalfa, cotton, rice, sorghum, and tomato.

Discussion.—*S. praefica* is dimorphic with a pale and a dark form. In the dark form the dorsal triangular markings blend into the ground color, and, as the larva becomes paler, the triangular markings become more evident. When identifying specimens from the western United States, one must be aware of the slight differences between *S. praefica* and *S. ornithogalli.* A key by Crumb (1927) included *S. praefica.*

Spodoptera marima (Schaus)

I received 2 adult specimens for identification from a farm near Riobamba, San Antonio, Ecuador that had been reared from corn (*Zea mays* L., Poaceae). The larvae were not preserved. This is the first record of a plant host for this species. Ruppel *et al.* (1957) list corn as a plant host of *S. ornithogalli* from Colombia. This is incorrect as *S. ornithogalli* does not occur in South America (Fig. 542). With this new information of *S. marima* feeding on corn, the record of *S. ornithogalli* from Colombia could be referable to *S. marima.* Another host record of *S. ornithogalli* from Colombia is cotton (*Gossypium* sp., Malvaceae) (Mowlam & Vega 1977) which could also be referable to *S. marima.*

Spodoptera ornithogalli (Guenée)

Figs. 154, 157, 516–518

Diagnosis.—Differences between *S. ornithogalli* and *S. praefica* were discussed under the latter. In the eastern United States, Mexico, and Central America, *S. ornithogalli* can be confused with *S. latifascia* and *S. dolichos.* The dorsal spot on

the mesothorax can be semicircular, elongate-oval, or triangular. The dorsal spot on the mesothorax is semicircular in *S. latifascia*, and trapezoidal in *S. dolichos*. In *S. ornithogalli* a thin white line, either solid or composed of dashes, passes through the dorsal triangular markings on the abdomen.

Description of preserved specimens.—*Head:* Color brown and black; reticulate; frons black; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax dorsolateral marking triangular (more semicircular on younger larvae); with lateral dark spot absent. Metathorax with dorsolateral mark elongate, narrow rectangle (absent on dark form, can be absent on early instar larvae); white spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Dorsolateral abdominal markings uniform in size on abdominal segments 1–8; marks narrow on segments 1–6, extending no more than half the distance between dorsolateral and middorsal stripe; each with a line passing through; mark on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present. Segments 2–6 without lateral dark spots in spiracular band. Spiracular band reticulate; spiracular band on segments 1–6 with white or light colored spot caudal to spiracle absent. Spiracles with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107 (range: 111–147; average: 123.3; n=10).

Color description.—Mature larva 20–36 mm in length. Head ground color brown suffused and all but concealed dorsally by deep fuscous, obscurely reticulate laterally; adfrontal areas and adjacent margin of head shield white. General ground color varying from pale gray to jet black. In well marked individuals, dorsal coloration consists of intermingled strands of pale and fuscous. Segmental spots triangular and dark, broadest about midlength, may be conspicuous on all abdominal segments or may be absent on all but segment 8. Dorsolateral stripe bright yellow or absent. Lateral band pale with pale and fuscous lines medially. Spiracular band fuscous. Subspiracular stripe of white flecks more or less suffused with orange or pinkish. Spiracles brownish with dark rims. Thoracic legs fuscous brown. Prolegs yellow, shields brown to dark fuscous (Crumb 1929, 1932).

Plant hosts.—*S. ornithogalli* is similar to *S. praefica* with 59 species of host plants in 21 families. Some of the more importantly affected crops include corn, cotton, lettuce, alfalfa, turnip, beet, bean, pea, and tomato. A single female specimen (USNMENT 142564) was reared from Assateague Island National Seashore, Maryland, on *Amaranthus pumilus* Rafinesque (Amaranthaceae) a federally listed threatened species.

Discussion.—*S. ornithogalli* is dimorphic with a pale and a dark form. In the dark form the dorsal triangular markings blend into the ground color, and as the larva becomes paler the triangular markings become more evident. In very dark individuals the dorsal triangles are absent.

Spodoptera pulchella (Herrich-Schäffer)

Figs. 162, 519–521

Diagnosis.—*S. pulchella* has a prominent brown lateral spot on the first abdominal segment with a conspicuous white dot caudad to the spiracle. There are no dorsal abdominal markings on the first segment and those on the second segment can be missing or are very narrow. The frons is brown in contrast to the lighter colored head.

Description of preserved specimens.—*Head:* Color brown; not reticulate; frons dark brown; cutting edge of mandible serrate; P2 setae farther apart than P1 setae; ratio ecdysial line: frons height, averages between 0.63–0.84. *Thorax:* Pronotum with dorsolateral stripe conspicuous, either solid or consisting of closely spaced spots and dashes; middorsal stripe narrower than dorsolateral stripe. Mesothorax with segmental spot trapezoidal; with lateral dark spot absent. Metathorax with segmental spot absent; lateral dark spot absent. *Abdomen:* Body smooth; setal pinacula minute. Middorsal stripe inconspicuous, narrower than dorsolateral stripe. Segmental spots on abdominal segments 7 and 8 larger than on 1–6; narrow on segments 1–6, extending no more than half the distance between dorsolateral and middorsal stripe; with narrow white dashes; on 8th abdominal segment larger than on mesothorax. Segment 1 with lateral dark spot present.

Segments 2–6 without lateral dark spots in spiracular band. Spiracular band reticulate; segments 1–6 in spiracular band with white or light colored spot caudal to spiracle present. Spiracles with black border and brown center; not stalked. Subspiracular stripe continuous through abdominal segment 1. Crochets uniordinal; total number on one side of body greater than 107.

Plant hosts.—The only known host plant is cotton from Puerto Rico (Fife 1939).

Color description.—Only known from preserved specimens.

Discussion.—The above description is based on five larvae preserved in alcohol. The specimens were reared from eggs obtained from two females collected in Florida, Dade Co., Homestead, January 4, 1989, by P. J. Landolt (collection in BMNH).

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Appendix I. Data matrix for 30 species of Spodoptera and 2 outgroup species used to produce the unordered trees (Figs. 1–2). *Galgula partita* Guenée was the designated outgroup and *Elaphria grata* Hübner was used to test the monophyly of *Spodoptera*. *Spodoptera* species are listed alphabetically. For character state descriptions see Phylogenetic Characters. Character states in bold should be coded as "10", but the limitations of Hennig86 allow only 10 character states per character. These characters were coded as their nearest neighbors on the cladogram (Figs. 1–2). Missing data were inferred by assigning character states based on nearest neighbors and are in italics (see text).

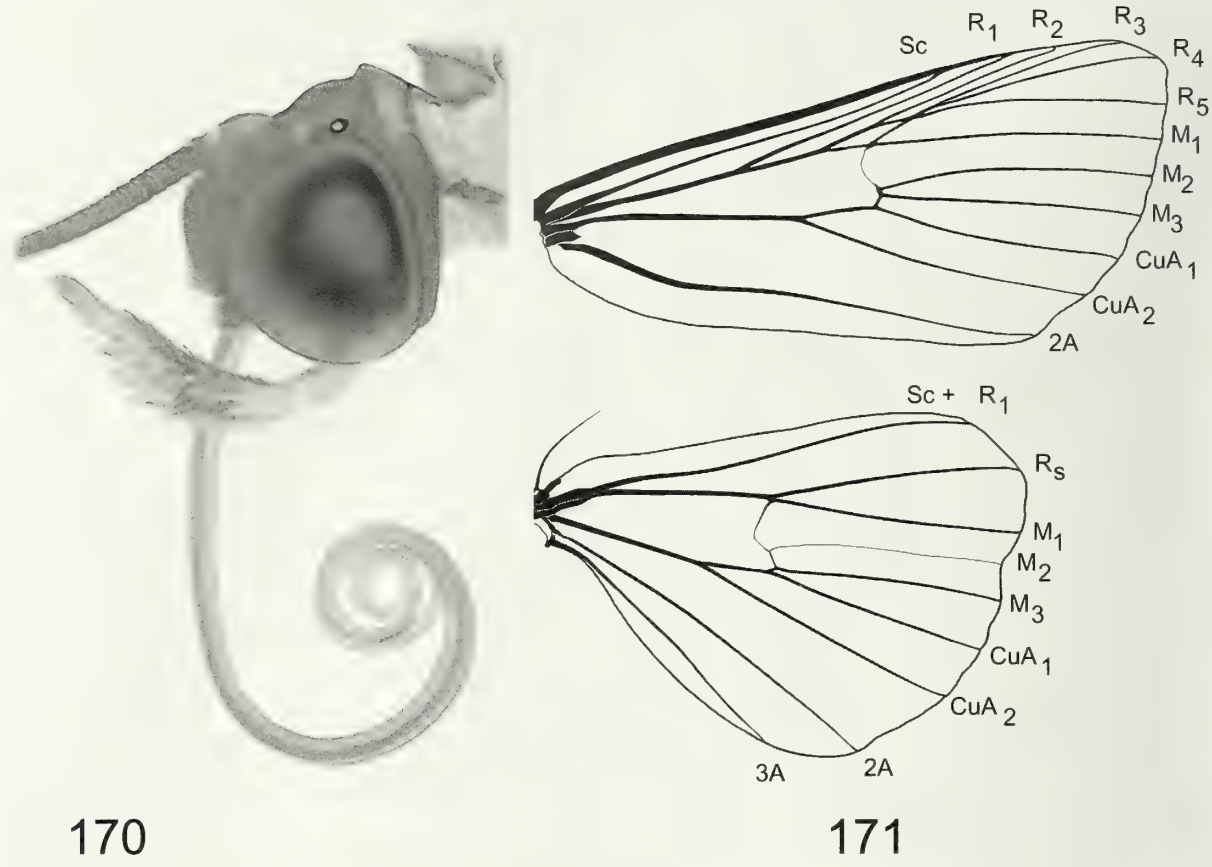
Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Taxon																								
Galgula	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Elaphria	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0
albula	0	0	3	2	2	2	1	1	2	3	4	1	2	0	0	0	2	5	4	3	1	2	4	0
androgea	0	0	1	2	1	0	1	1	3	8	5	3	9	1	1	1	2	7	6	9	1	3	0	0
apertura	2	0	0	2	1	0	2	1	4	7	3	2	7	0	0	0	1	2	1	2	1	1	0	0
cilium	2	0	2	3	1	0	3	2	4	6	2	1	4	0	0	0	1	3	2	3	1	2	3	0
compta	0	0	0	2	2	1	1	1	3	3	4	1	2	0	0	0	2	6	3	3	1	2	4	0
cosmiodes	0	0	1	2	1	0	6	1	3	9	9	4	8	1	1	1	3	9	7	**9**	1	2	6	1
depravata	1	0	2	3	1	0	3	2	4	6	1	1	4	0	0	0	1	3	3	3	1	2	0	0
descoinsi	0	0	1	2	1	0	6	1	3	9	9	4	8	1	1	1	3	9	7	**9**	1	2	6	1
dolichos	0	0	1	2	1	0	1	1	3	8	5	3	**9**	1	1	1	3	7	6	9	1	3	0	0
eridania	0	0	0	2	2	2	4	1	3	3	4	1	2	0	0	0	2	5	3	3	1	2	4	0
evanida	0	0	0	2	1	0	6	1	3	9	9	4	8	1	1	1	3	8	7	3	1	2	5	1
exempta	0	0	1	2	1	0	7	1	4	5	2	1	3	0	0	0	2	5	3	5	1	1	2	0
exigua	0	0	2	2	1	0	0	0	4	2	1	1	3	0	0	0	2	4	5	4	1	2	0	0
frugiperda	0	0	1	2	1	0	1	1	5	8	6	2	3	1	1	1	2	7	3	8	1	2	0	0
latifascia	0	0	1	2	1	0	6	1	3	9	9	4	8	1	1	1	3	8	7	**9**	1	2	7	1
littoralis	0	0	1	2	1	0	5	1	3	8	6	2	5	1	1	1	3	7	6	9	1	1	0	0
litura	0	0	1	2	1	0	5	1	5	8	7	2	5	1	1	1	3	8	6	9	1	1	8	0
malagasy	2	0	0	2	1	0	2	1	4	7	3	2	7	0	0	0	1	2	1	2	1	1	0	0
marima	0	0	1	2	1	0	1	1	5	8	8	5	6	1	1	1	3	7	8	8	1	2	5	1
mauritia	0	1	1	3	1	0	3	3	4	8	2	2	3	0	0	0	2	5	0	6	1	1	0	0
ochrea	0	0	3	2	2	1	1	1	2	4	4	1	2	0	0	0	2	5	3	3	1	2	4	0
ornithogalli	0	0	1	2	1	0	1	1	5	8	8	5	6	1	1	1	3	7	8	8	1	2	5	1
pecten	1	0	2	3	1	0	3	2	4	6	1	1	4	0	0	0	1	3	3	3	1	1	0	0
pectinicornis	1	0	0	2	1	0	3	1	4	7	3	2	7	0	0	0	1	2	*1*	2	1	1	0	0
picta	0	0	0	2	1	0	5	1	3	8	7	2	5	1	1	1	3	8	6	9	1	1	8	0
praefica	0	0	0	2	1	0	8	1	5	8	8	5	6	1	1	1	2	7	8	8	1	2	5	1
pulchella	0	0	1	2	1	0	1	1	5	8	8	5	6	1	1	1	3	7	8	9	1	2	5	1
roseae	1	0	4	2	1	0	1	1	5	8	8	5	6	1	1	1	3	7	8	9	1	2	5	1
triturata	0	1	1	3	1	0	2	3	4	8	2	1	3	0	0	0	2	5	0	7	1	1	0	0
umbraculata	1	0	0	4	1	0	3	1	4	6	2	1	7	0	0	0	1	3	3	3	1	1	0	0

Appendix II. Data matrix for 30 species of Spodoptera and 2 outgroup species used to produce the Transformation Series Analysis (TSA) trees (Fig. 3). *Galgula partita* Guenée was the designated outgroup and *Elaphria grata* Hübner was used to test the monophyly of *Spodoptera*. *Spodoptera* species are listed alphabetically. For character state descriptions see Phylogenetic Characters. Character states are coded using ordinal coding to define the character state tree for each character (see text). Due to the complex nature of some character state trees, as many as 5 "states" can define a single character state from Appendix I. Missing data were inferred by assigning character states based on nearest neighbors and are in italics (see text).

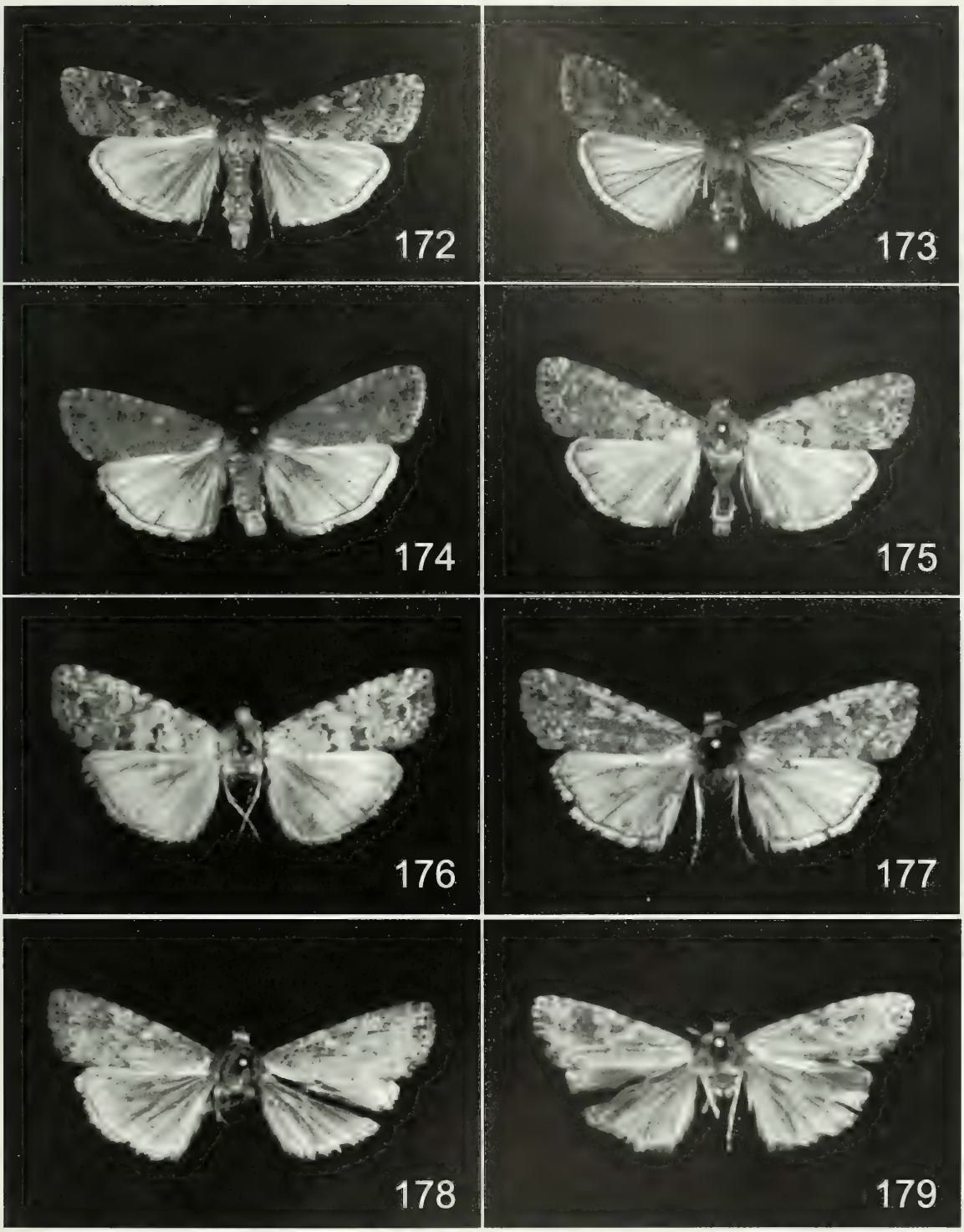
Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Taxon																								
Galgula	0	0	20	00	0	0	0010	00	10	0000	0110	01	01111	0	0	0	00	01	110	01000	0	00	1110	0
Elaphria	0	0	20	10	0	0	0010	00	00	1000	0110	11	10111	0	0	0	00	11	110	11000	0	00	1111	0
albula	0	0	21	20	2	2	1010	10	21	3100	1210	11	12111	0	0	0	10	31	211	31000	1	10	1101	0
androgea	0	0	10	20	1	0	1010	10	30	3000	2100	20	11110	1	1	1	10	41	310	23000	1	11	1111	0
apertura	2	0	20	20	1	0	3010	10	20	5000	1111	21	11101	0	0	0	20	33	220	41000	1	20	1111	0
cilium	2	0	30	30	1	0	2010	20	20	4000	1110	11	21111	0	0	0	20	32	200	31000	1	10	1011	0
compta	0	0	20	20	2	1	1010	10	30	3100	1210	11	12111	0	0	0	10	30	*210*	31000	1	10	1101	0
cosmiodes	0	0	10	20	1	0	3011	10	30	3001	4110	31	11121	1	1	1	11	61	510	21001	1	10	2112	1
depravata	1	0	30	30	1	0	2010	20	20	4000	1010	11	21111	0	0	0	20	32	210	31000	1	10	1111	0
descoinsi	0	0	10	20	1	0	3011	10	30	3001	4110	31	11121	1	1	1	11	61	510	21001	1	10	2112	1
dolichos	0	0	10	20	1	0	1010	10	30	3000	2100	20	11112	1	1	1	11	41	310	23000	1	11	1111	0
eridania	0	0	20	20	2	2	1110	10	30	3100	1210	11	12111	0	0	0	10	31	210	31000	1	10	1101	0
evanida	0	0	20	20	1	0	3011	10	30	3001	4110	31	11121	1	1	1	11	51	510	31000	1	10	2111	1
exempta	0	0	10	20	1	0	4010	10	20	3010	1110	11	11111	0	0	0	10	31	210	20000	1	20	1211	0
exigua	0	0	30	20	1	0	0010	00	20	2000	1010	11	11111	0	0	0	10	21	010	21000	1	10	1111	0
frugiperda	0	0	10	20	1	0	1010	10	40	3000	2110	21	11111	1	1	1	10	41	210	22000	1	10	1111	0
latifascia	0	0	10	20	1	0	3011	10	30	3001	4110	31	11121	1	1	1	11	51	510	21001	1	10	3111	1
littoralis	0	0	10	20	1	0	3020	10	30	3000	2110	21	11011	1	1	1	11	41	310	23000	1	20	1111	0
litura	0	0	10	20	1	0	3020	10	40	3000	2120	21	11011	1	1	1	11	51	310	23000	1	20	1121	0
malagasy	2	0	20	20	1	0	3010	10	20	5000	1111	21	11101	0	0	0	20	33	220	41000	1	20	1111	0
marima	0	0	10	20	1	0	1010	10	40	3000	3110	41	11211	1	1	1	11	41	410	22000	1	10	2111	1
mauritia	0	1	10	30	1	0	3010	11	20	3000	1110	21	11111	0	0	0	10	31	110	21100	1	20	1111	0
ochrea	0	0	21	20	2	1	1010	10	21	3200	1210	11	12111	0	0	0	10	31	210	31000	1	10	1101	0
ornithogalli	0	0	10	20	1	0	1010	10	40	3000	3110	41	11211	1	1	1	11	41	410	22000	1	10	2110	1
pecten	1	0	30	30	1	0	2010	20	20	4000	1010	11	21111	0	0	0	20	32	210	31000	1	20	1111	0
pectinicornis	1	0	20	20	1	0	2010	10	20	5000	1111	21	11101	0	0	0	20	33	*220*	41000	1	20	1111	0
picta	0	0	20	20	1	0	3020	10	30	3000	2120	21	11011	1	1	1	11	51	310	23000	1	20	1121	0
praefica	0	0	20	20	1	0	3000	10	40	3000	3110	41	11211	1	1	1	10	41	410	22000	1	10	2111	1
pulchella	0	0	10	20	1	0	1010	10	40	3000	3110	41	11211	1	1	1	11	41	410	23000	1	10	2110	1
roseae	1	0	00	20	1	0	1010	10	40	3000	3110	41	11211	1	1	1	11	41	410	23000	1	10	2111	1
triturata	0	1	10	30	1	0	3010	11	20	3000	1110	11	11111	0	0	0	10	31	110	21010	1	20	1111	0
umbraculata	1	0	20	21	1	0	2010	10	20	4000	1110	11	11101	0	0	0	20	32	210	31000	1	20	1111	0

Appendix III. Character number (character state) are listed below for character state changes traced on the phylogenetic tree in Fig. 3. Characters and states are listed in Appendices I & II. Numbers on Fig. 3 represent the clades below. Synapomorphic character states are in regular type and homoplasious character states are in italics. Characters with more than one state are unresolved at that clade.

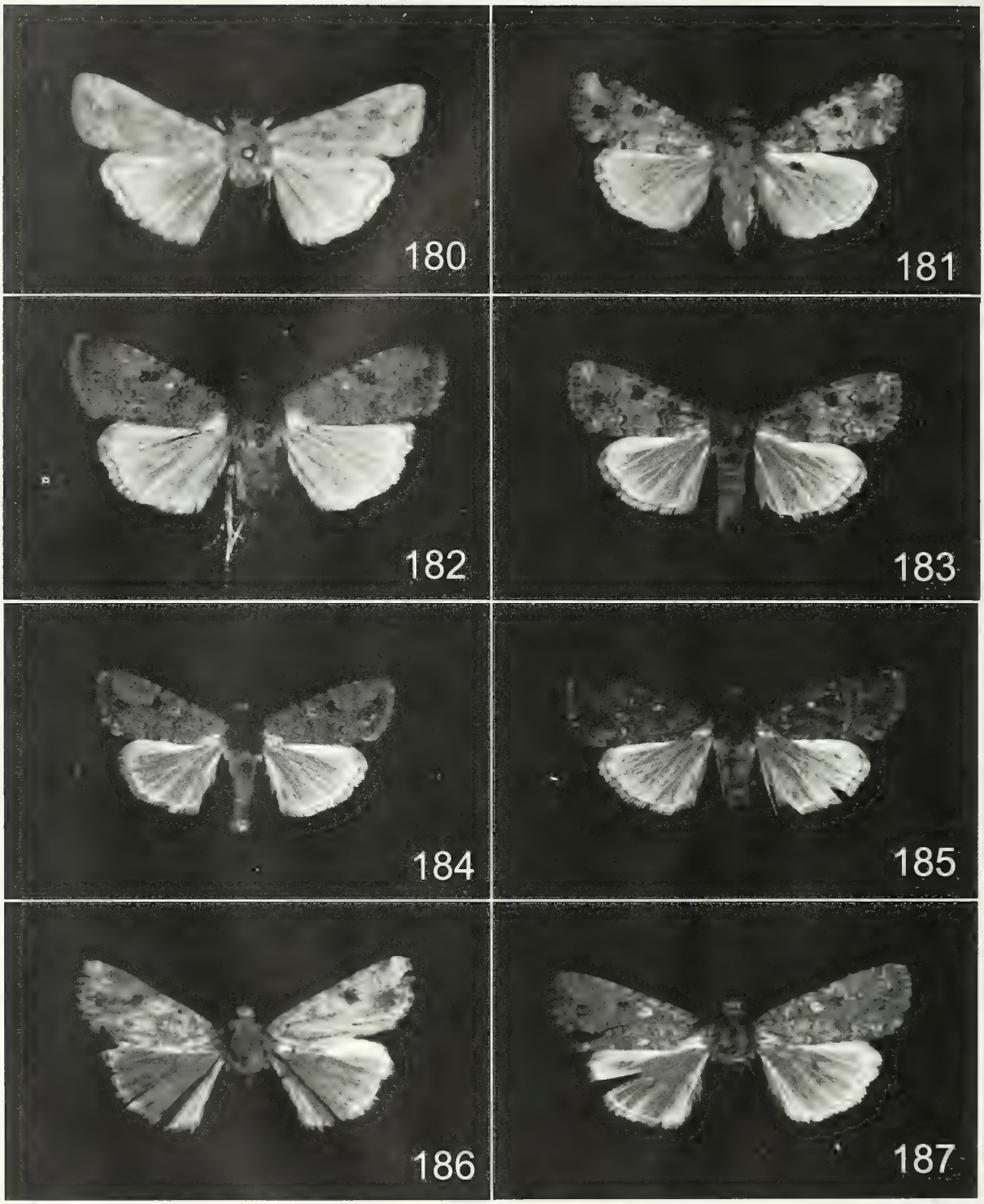
Clade 1: 1(0), 2(0), *3(0)*, 4(0), 5(0), 6(0), 7(0), 8(0), 9(1), 10(0/1/2/3/6/8), 11(0), 12(1), 13(1/3), 14(1), 15(0), 16(0), 17(0), 18(0), *19(0)*, 20(1), 21(0), 22(0), 23(1), 24(0)
Galgula: 10(1), 13(1)
Clade 2: 4(2), 5(1), 9(4), 11(2), 12(2), 13(3), 14(0), *17(2)*, 18(4), *20(4)*, 21(1), 22(2)
Elaphria: 9(0), 10(0), 12(0), 13(0), 18(1), 20(0), 23(0)
Clade 3: 18(5)
exigua: *3(2)*, 4(1), 10(2), *11(1)*, 19(5)
Clade 4: 7(1), 8(1), 19(3)
Clade 20: *20(3)*
Clade 21: 5(2), 6(1), 10(3), 11(4), 13(2), 23(4)
eridania: *6(2)*, 7(4)
albula: *6(2)*, 19(4)
Clade 22: 9(2)
compta: 18(6)
Clade 23: 3(3), 9(3)
ochrea: 10(4)
Clade 24: *1(1)*, *7(3)*, 10(6), 17(1), 18(3)
Clade 25 (*cilium* species group): *3(2)*, *4(3)*, 8(2), 13(4)
cilium: *1(2)*, 19(2), 23(3)
Clade 26: None
pecten: *11(1)*, *22(1)*
depravata: *11(7)*
Clade 27: (*umbraculata* species group): 13(7), *22(1)*
umbraculata: 4(4)
Clade 28: 10(7), 11(3), *12(3)*, 18(2), 19(1), 20(2)
Clade 29: *1(2)*, *7(2)*
apertura: *3(1)*
Clade 5: *3(1)*, 10(8), *12(3)*, *20(8)*
Clade 18 (*exempta* species group): *22(1)*
exempta: *7(7)*, 10(5), 20(5), 23(2)
Clade 19: 2(1), *4(3)*, 8(3), *11(7)*, *19(0)*
mauritia: *7(3)*, 20(6)
triturata: *7(2)*, 20(7)
Clade 6: 9(3), 11(6), 15(1), 16(1), 18(7), *20(8/9)*
frugiperda: *9(5)*
Clade 7: 12(3/4), 17(2/3), 19(6), 22(3)
Clade 17 (*dolichos* species group): 11(5), 12(4), *20(9)*
dolichos: 13(10), *17(3)*
androgea: 13(9), *17(2)*
Clade 8: 11(8), 12(5), *17(3)*, 19(7), *20(8)*, 23(5), 24(1)
Clade 15 (*littoralis* species group): 7(5), *12(3)*, 13(5), *20(9)*, *22(1)*
Clade 16: *18(8)*, 23(8)
Clade 12 (*evanida* species group): 7(6), 10(9), 11(9), 13(8), *18(8)*, *20(4)*
evanida: *3(0)*,
Clade 13: 20(10)
evanida: *20(3)*
latifascia: 23(8)
Clade 14: 18(9), 23(6)
Clade 9 (*praefica* species group): *9(5)*, 12(6), 13(6), 19(8)
praefica: *3(0)*, 7(8), *17(2)*
Clade 10: None
marima: *18(8)*
Clade 11: *20(9)*
roseae: *1(1)*, 3(4)



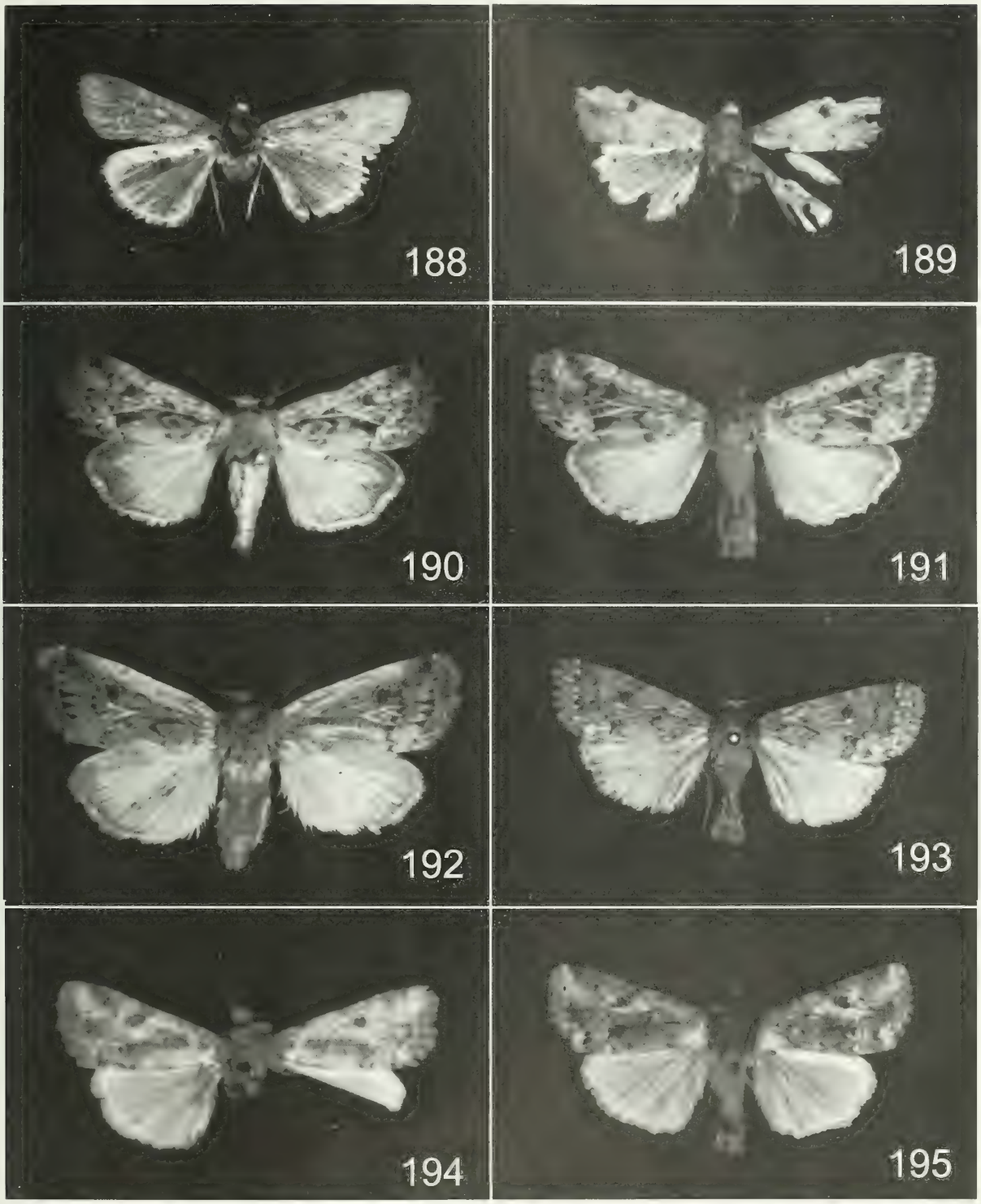
Figs. 170–171. *Spodoptera mauritia* (Boisduval). 169, Head. 170, Wing venation.



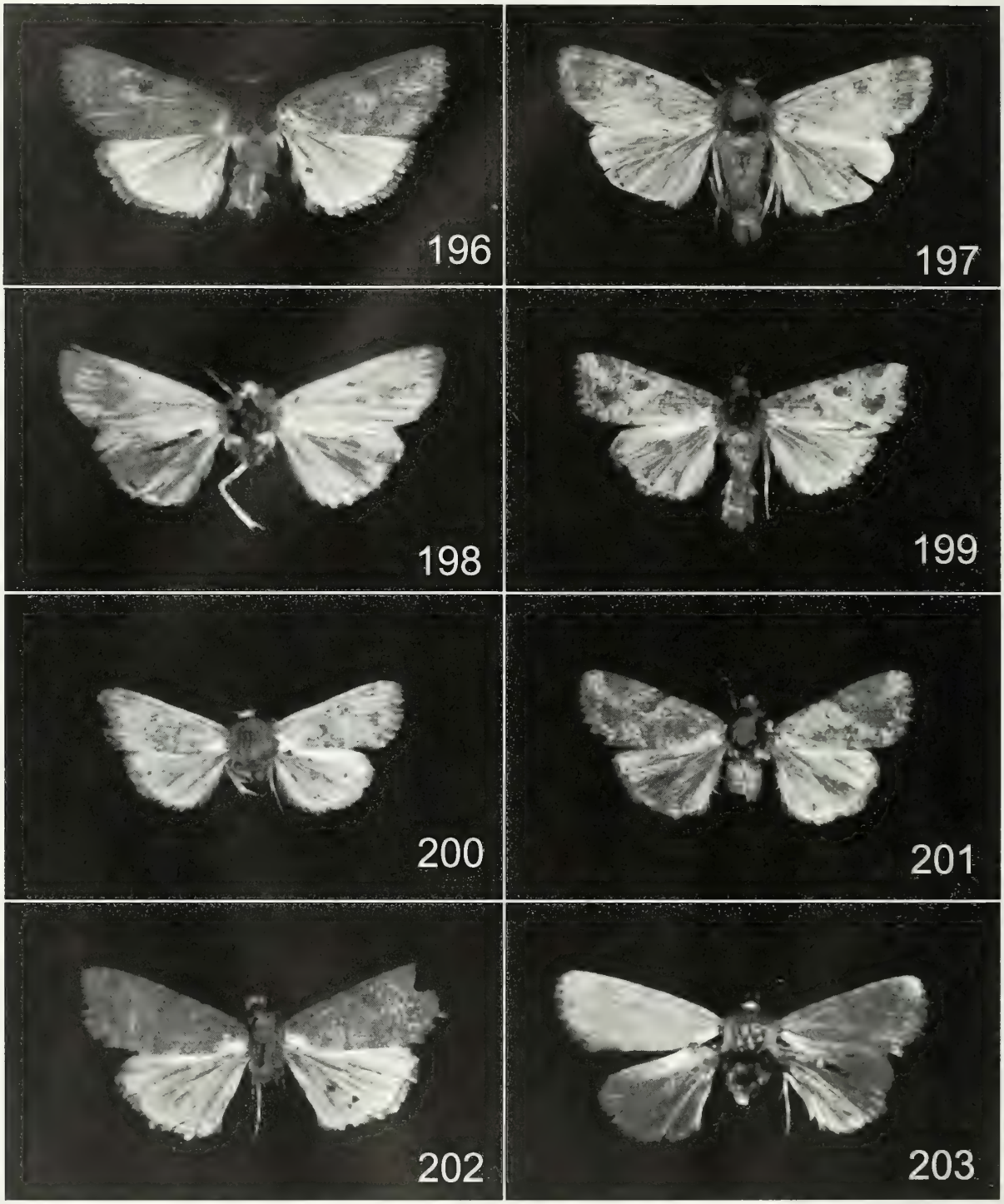
Figs. 172–179. *S. exigua* (Hübner). 172, ♀, Arizona, USNMENT 57321 (USNM). 173, ♀, Mississippi, USNMENT 60966 (USNM). 174, ♀, Texas, USNMENT 56829 (USNM). 175, ♂ Paralectotype, *Laphygma exigua* subsp. *antipodea* Warren, synonym of *S. exigua*, Australia, (BMNH). 176, ♂ Lectotype, *Laphygma exigua* subsp. *antipodea* Warren, synonym of *S. exigua*, Australia, (BMNH). 177, ♂ Holotype, *Laphygma caradrinoides* Walker, synonym of *S. exigua*, C. Colony, (BMNH). 178, ♂ Lectotype, *Caradrina flavimaculata* Harvey, synonym of *S. exigua*, California, (BMNH). 179, ♂ Lectotype, *Caradrina junceti* Zeller, synonym of *S. exigua*, Spain, (BMNH).



Figs. 180–187. *Spodoptera* spp. 180, ♂,*Caradrina flavimaculata* Harvey, synonym of *S. exigua*, California, (BMNH). 181, ♂ Neotype, *S. cilium* Guenée, South Africa, USNMENT 61924 (USNM). 182, ♀, *S. cilium* Guenée, South Africa, USNMENT 61919 (USNM). 183, ♂,*S. cilium* Guenée, Madagascar, (MNHN). 184, ♀, *S. cilium* Guenée, Madagascar, (MNHN). 185, ♀, *S. cilium* Guenée, Madagascar, (MNHN). 186, ♂, *Caradrina insignata* Walker, synonym of *S. cilium* , South Africa, (BMNH). 187, ♀, *Caradrina orbicularis* Walker, Lectotype, synonym of *S. cilium* , South Africa, (BMNH).

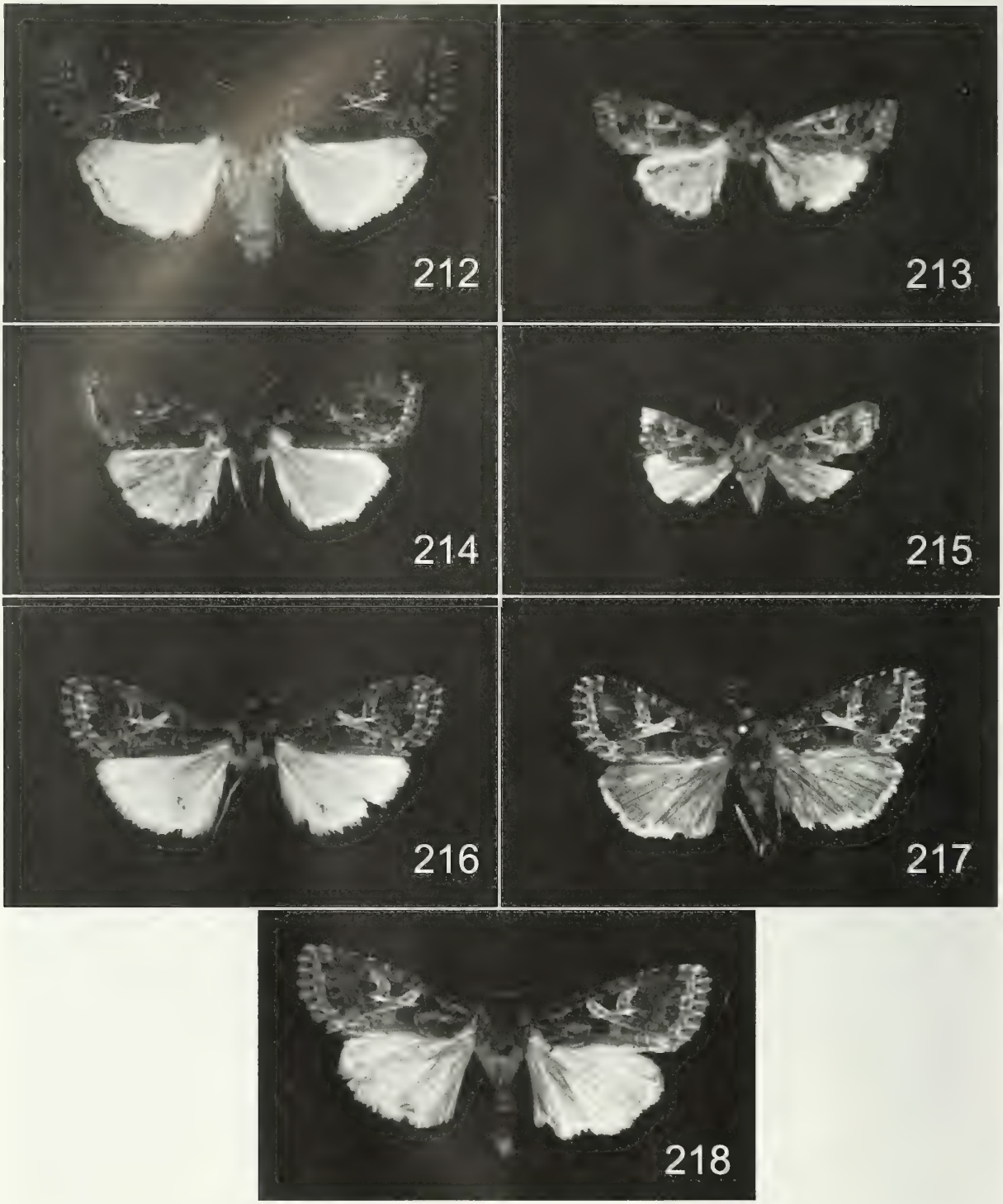


Figs. 188–195. *Spodoptera* spp. 188, ♀ Lectotype, *Caradrina praeterita* Walker, synonym of *S. cilium* , South Africa, (BMNH). 189, ♂ Holotype, *Laphygma procedens* Walker, synonym of *S. cilium*, Sierra Leone, (BMNH). 190, ♂, *S. depravata* (Butler), Japan, (BMNH). 191, ♂, *S. depravata*, Lectotype, Japan, (BMNH). 192, ♂, *S. depravata* (Butler), China, (BMNH). 193, ♀, *S. depravata* (Butler), Japan, (BMNH). 194, ♂ Holotype, *S. pecten* Guenée, Java, (BMNH). 195, ♂, *S. pecten* Guenée, Philippines, USNMENT 65923 (USNM).

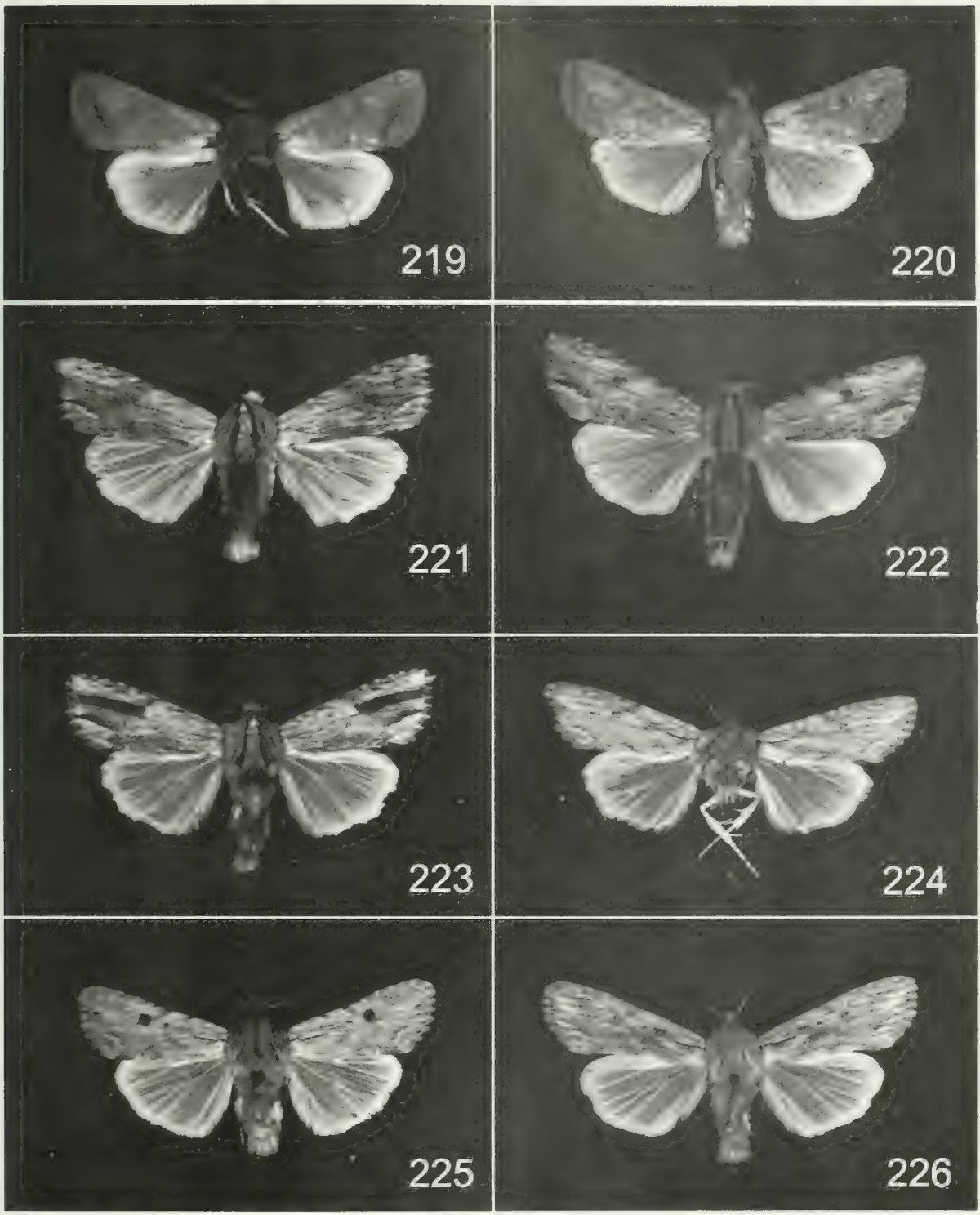


Figs. 196–203. *Spodoptera pecten* Guenée. 196, ♀, *S. pecten* Guenée, Philippines, USNMENT 65924 (USNM). 197, ♂, *S. erica* Butler, synonym of *S. pecten*, Formosa [Taiwan], (BMNH). 198, ♀ Lectotype, *S. erica* Butler, synonym of *S. pecten*, Formosa [Taiwan], (BMNH). 199, ♂, *Agrotis infixa* Walker, synonym of *S. pecten*, Borneo, (BMNH). 200, ♀, *Spodoptera insulsa* Walker, synonym of *S. pecten*, Java, (BMNH). 201, ♂ Holotype, *Caradrina pectinata* Hampson, synonym of *S. pecten*, Naga Hills [India], (BMNH). 202, ♀ Lectotype, *Elydna speciosa* Rothschild, synonym of *S. pecten*, Western Sumatra [Indonesia], (BMNH). 203, ♀, Lectotype, *Spaelotis uniformis* Swinhoe synonym of *S. pecten*, Burma, (BMNH).

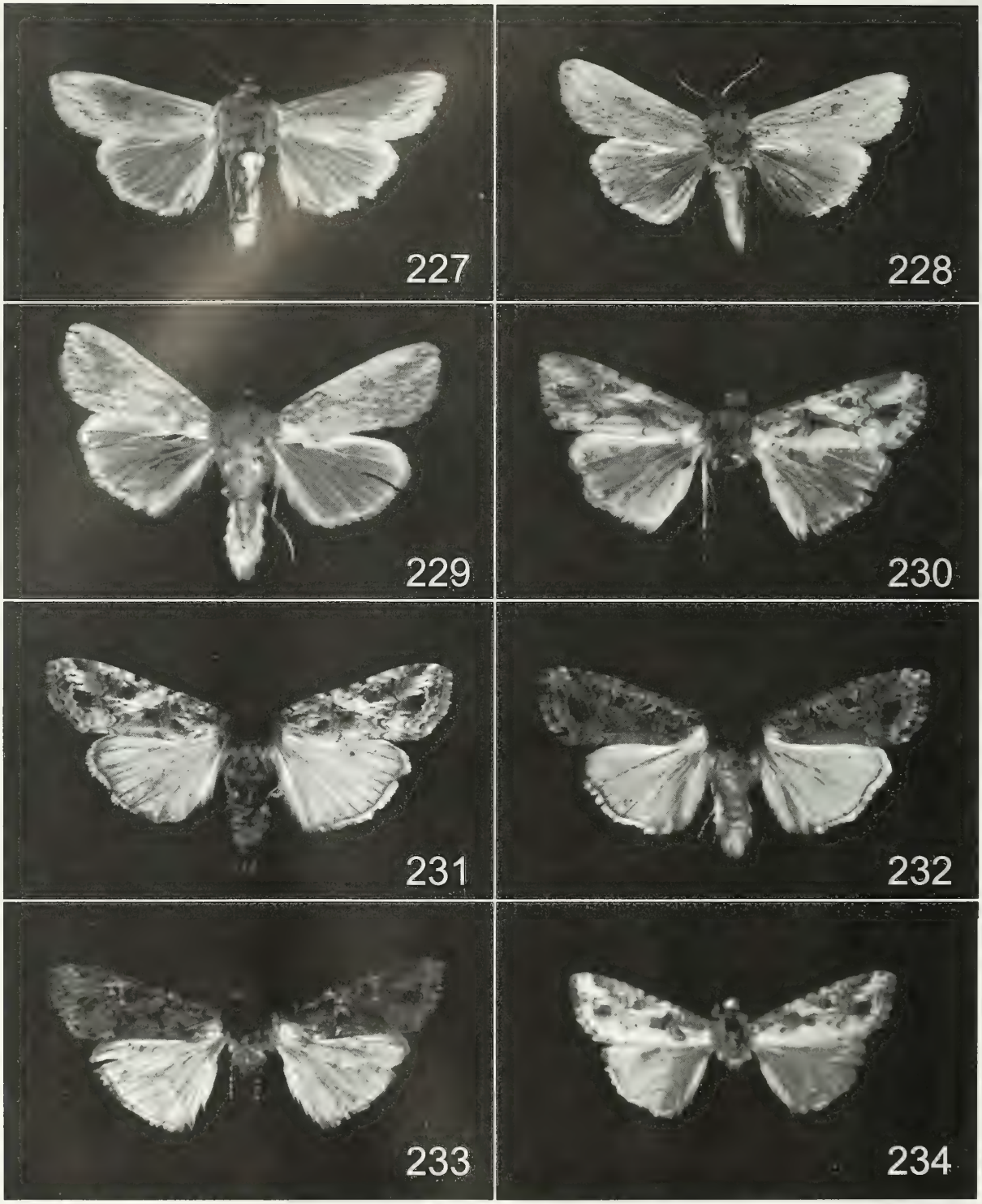
Figs. 204–211. *Spodoptera* spp. 204, ♂ Holotype, *S. umbraculata* (Walker), Australia, (BMNH). 205, ♂, *S. umbraculata*, Australia, (ANIC). 206, ♀, *S. umbraculata*, Australia, (ANIC). 207, ♂ Lectotype, *S. pectinicornis* (Hampson), Ceylon [Sri Lanka], (BMNH). 208, ♂, *S. pectinicornis*, Bangladesh, USNMENT 62934 (BMNH). 209, *S. pectinicornis*, ♂, Ceylon [Sri Lanka], USNMENT 62933 (BMNH). 210, ♀, *S. pectinicornis*, Ceylon [Sri Lanka], USNMENT 62936 (BMNH). 211, ♂ Lectotype, *Caradrina hennia* Swinhoe, synonym of *S. pectinicornis*, Sarawak, (BMNH).]



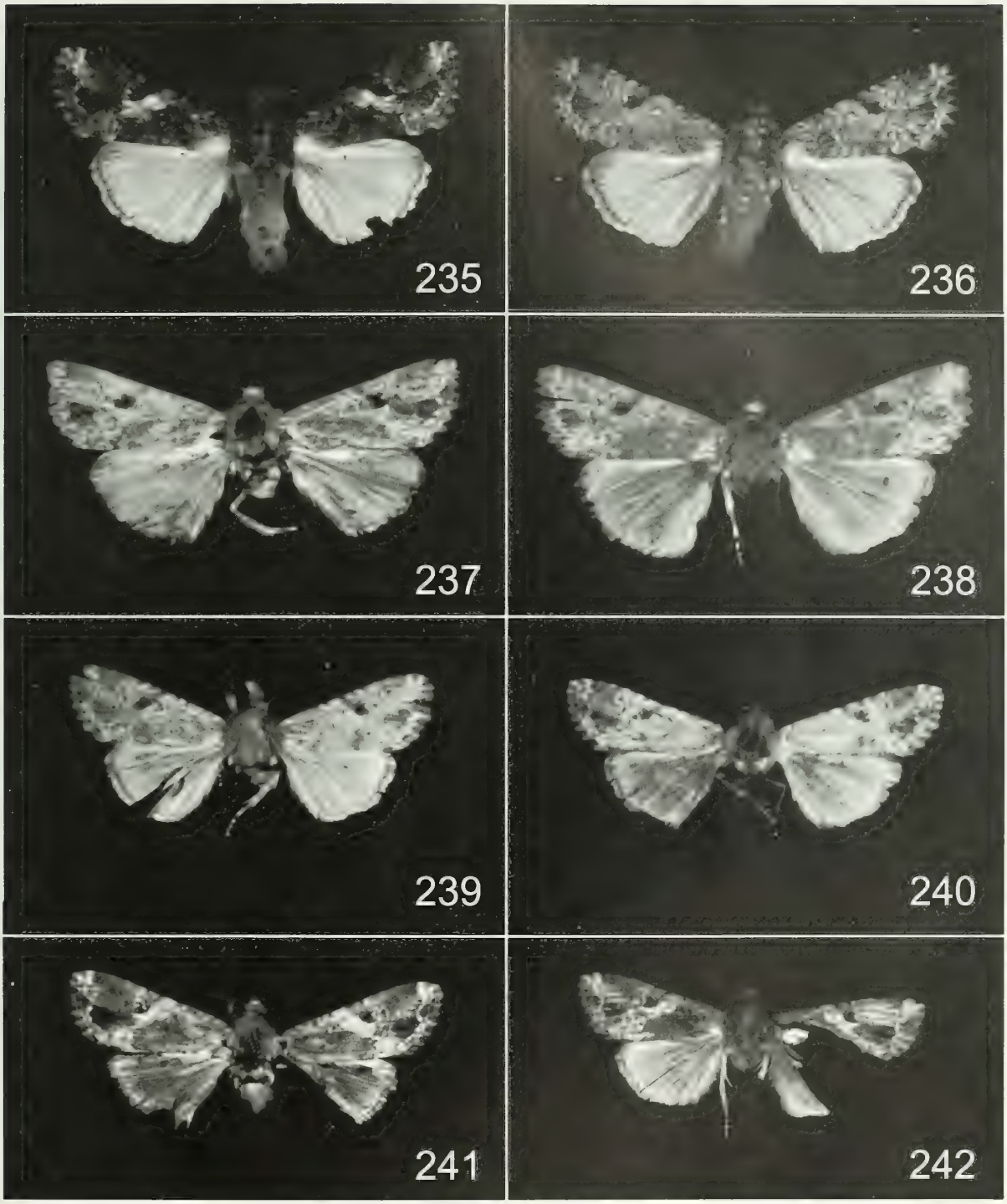
Figs. 212–218. *Spodoptera* spp. 212, ♀ Neotype, *S. apertura* (Walker), Australia, (ANIC). 213, ♂ Lectotype, *Laphygma connexa* Wileman, synonym of *S. apertura*, Formosa [Taiwan], (BMNH). 214, ♂ Lectotype, *Laphygma leucophlebia* Hampson, synonym of *S. apertura*, Natal, (BMNH). 215, ♂ Lectotype, *Prodenia synstictis* Hampson, synonym of *S. apertura*, Ceylon [Sri Lanka], (BMNH). 216, ♂ Holotype, *Spodoptera teferri* Laporte, synonym of *S. apertura*, Ethiopia, (MNHN). 217, ♂ Holotype, *S. malagasy* Viette, Madagascar, (MNHN). 218, ♀, *S. malagasy*, Madagascar, (BMNH).



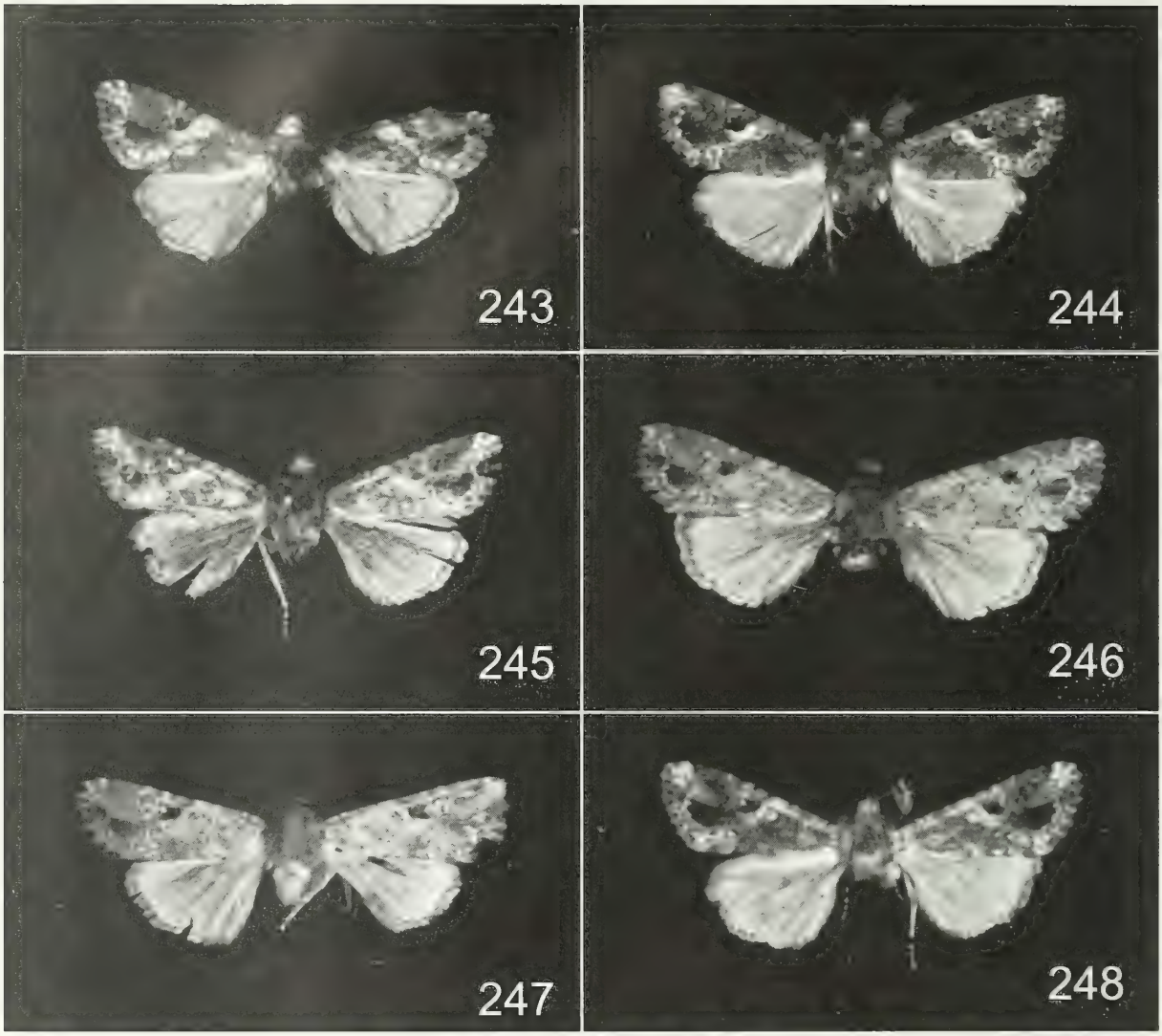
Figs. 219–226. *Spodoptera* spp. 219, ♂, *S. compta* (Walker), Peru, (BMNH). 220, ♂, *S. compta*, Peru, (BMNH). 221, ♀, *S. eridania* (Stoll), Florida, USNMENT 57644 (USNM). 222, ♂ Neotype, *S. eridania*, Florida, USNMENT 57649 (USNM). 223, ♂, *S. eridania*, Florida, USNMENT 57648 (USNM). 224, ♂, *S. albula* (Walker), St. Domingo, (BMNH). 225, ♂, *S. albula*, Texas, USNMENT 61180 (USNM). 226, ♀, *S. albula*, Florida, USNMENT 61148 (USNM).



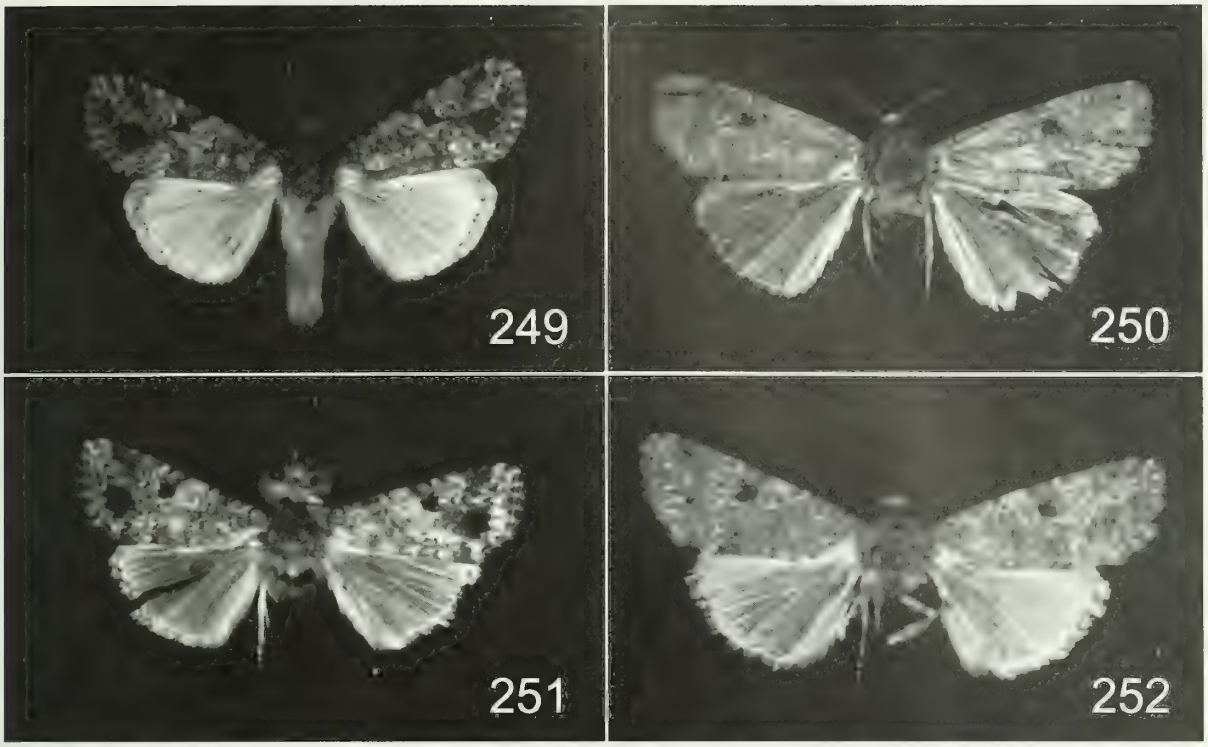
Figs. 227–234. *Spodoptera* spp. 227, ♂, Lectotype, *S. ochrea* (Hampson) Peru, (BMNH). 228, ♂, *S. ochrea*, Peru, USNMENT 65921 (USNM). 229, ♂, *S. ochrea*, Peru, USNMENT 65922 (USNM). 230, ♂ Holotype, *S. exempta* (Walker), No locality label, (BMNH). 231, ♂, *S. exempta*, Hawaii, USNMENT 65925 (USNM). 232, ♀, *S. exempta*, Australia, USNMENT 65926 (USNM). 233, ♀ Holotype, *Prodenia bipars* Walker, synonym of *S. exempta*, Australia, (BMNH). 234, ♂ Holotype, *Prodenia ingloria* Walker, synonym of *S. exempta*, Australia, (BMNH).



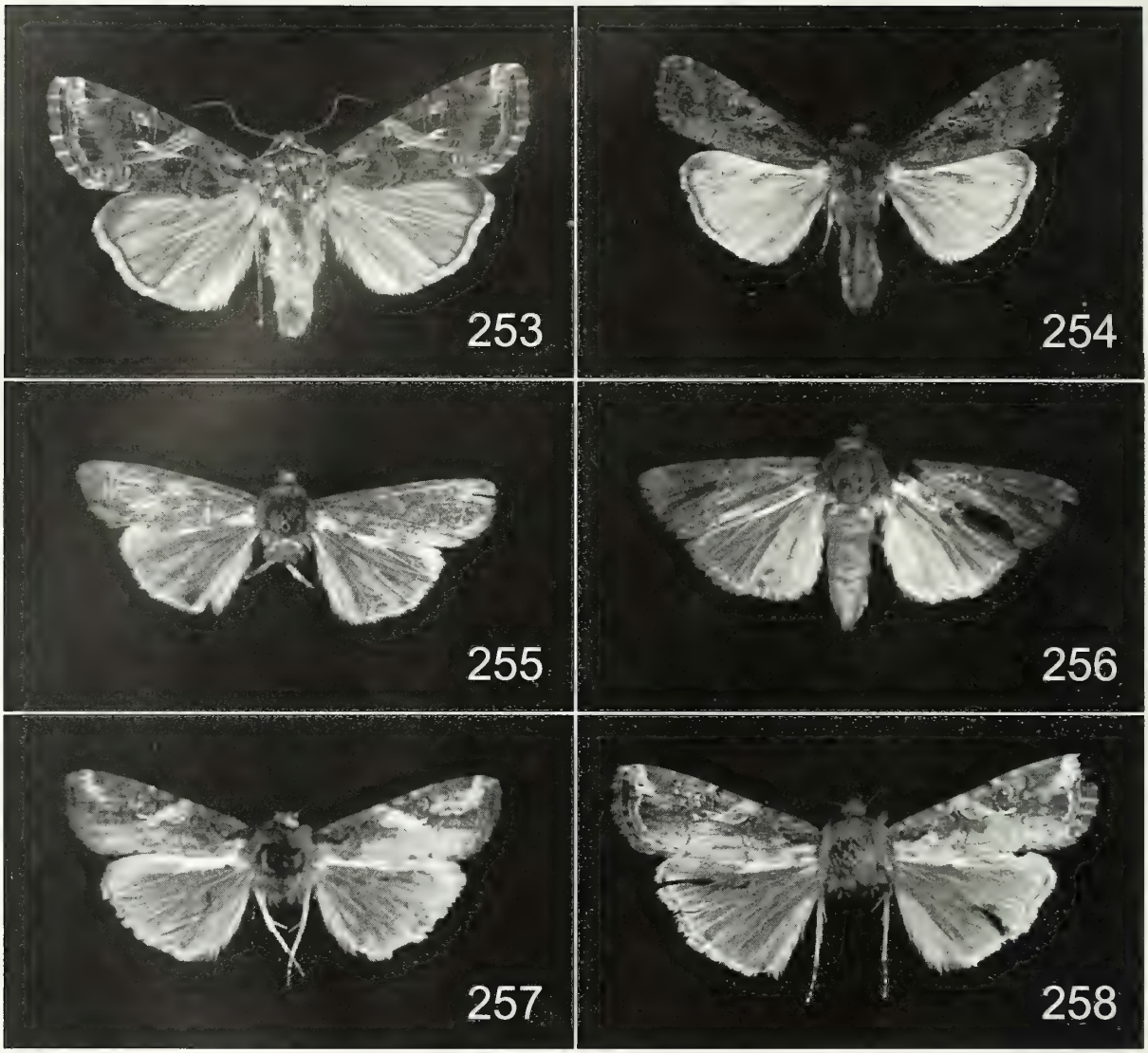
Figs. 235–242. *Spodoptera mauritia* (Boisduval). 235, ♂ Neotype, New Caledonia, USNMENT 65927 (USNM). 236, ♀, New Caledonia, USNMENT 65928 (USNM). 237, ♀ Holotype, *Agrotis aliena* Walker, synonym of *S. mauritia,* Mauritius, (BMNH). 238, ♀ Holotype, *Agrotis bisignata* Walker, synonym of *S. mauritia,* Australia, (BMNH). 239, ♀ Lectotype, *Spodoptera filum* Guenée, synonym of *S. mauritia,* Java [Indonesia], (BMNH). 240, ♀, *Prodenia infecta* Walker, synonym of *S. mauritia,* N. India, (BMNH). 241, ♂ Holotype, *Prodenia insignata* Walker, synonym of *S. mauritia,* N. India, (BMNH). 242, ♂ Lectotype ♂, *Spodoptera nubes* Guenée, synonym of *S. mauritia,* No locality label, (BMNH).



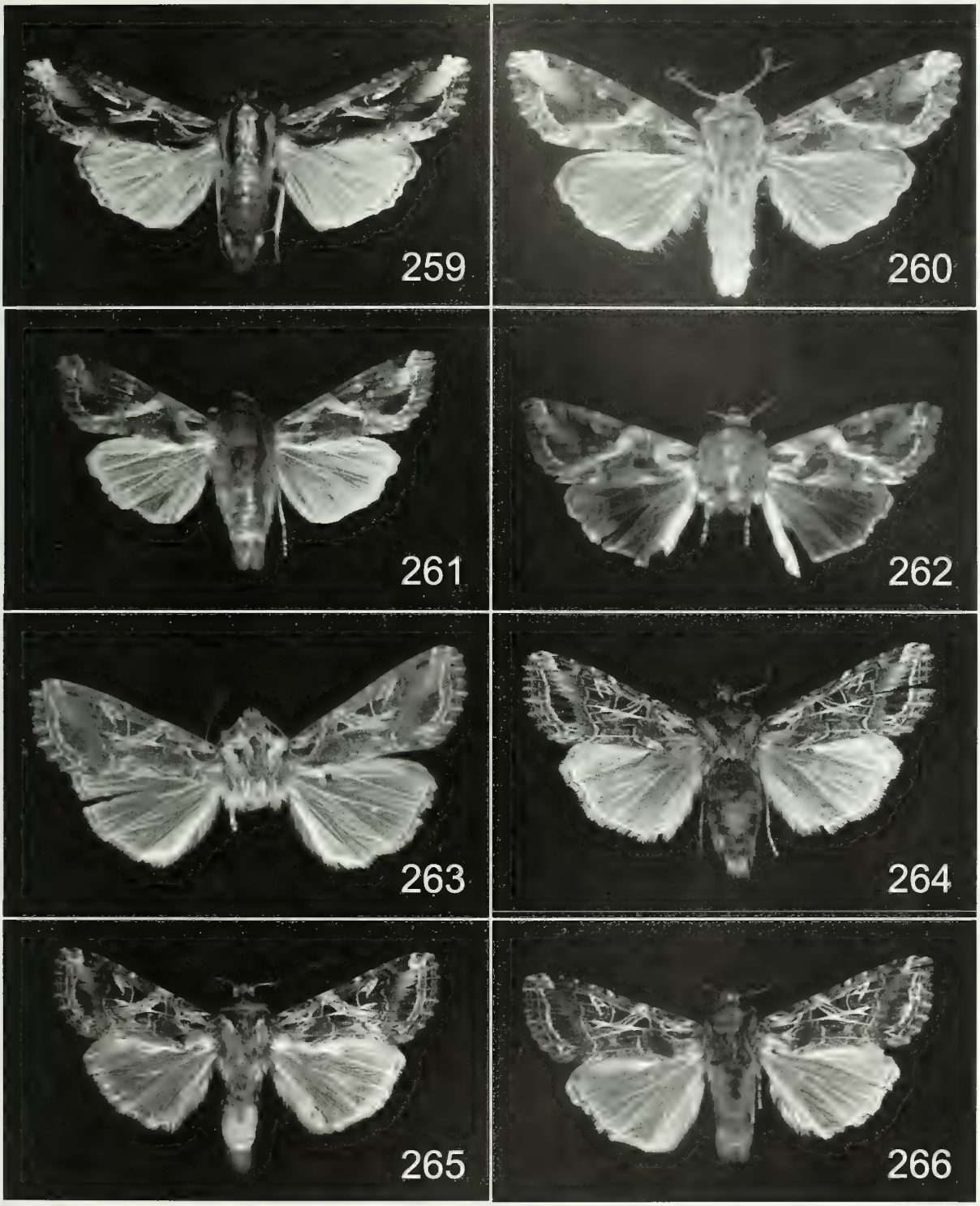
Figs. 243–248. *Spodoptera mauritia* (Boisduval). 243, ♂ Holotype, *Hadena obliqua* Walker, synonym of *S. mauritia,* Shanghai [China], (BMNH). 244, ♂ Holotype, *Prodenia permunda* Walker, synonym of *S. mauritia,* Siam [Thailand], (BMNH). 245, ♂ Holotype, *Laphygma squalida* Walker, synonym of *S. mauritia,* N. India, (BMNH). 246, ♀ Holotype, *Agrotis submarginalis* Walker, *S. mauritia,* Java [Indonesia], (BMNH). 247, ♀ Holotype, *Agrotis transducta* Walker, synonym of *S. mauritia,* Ceylon [Sri Lanka], (BMNH). 248, ♂ Holotype, *Prodenia venustula* Walker, synonym of *S. mauritia,* S. India, (BMNH).



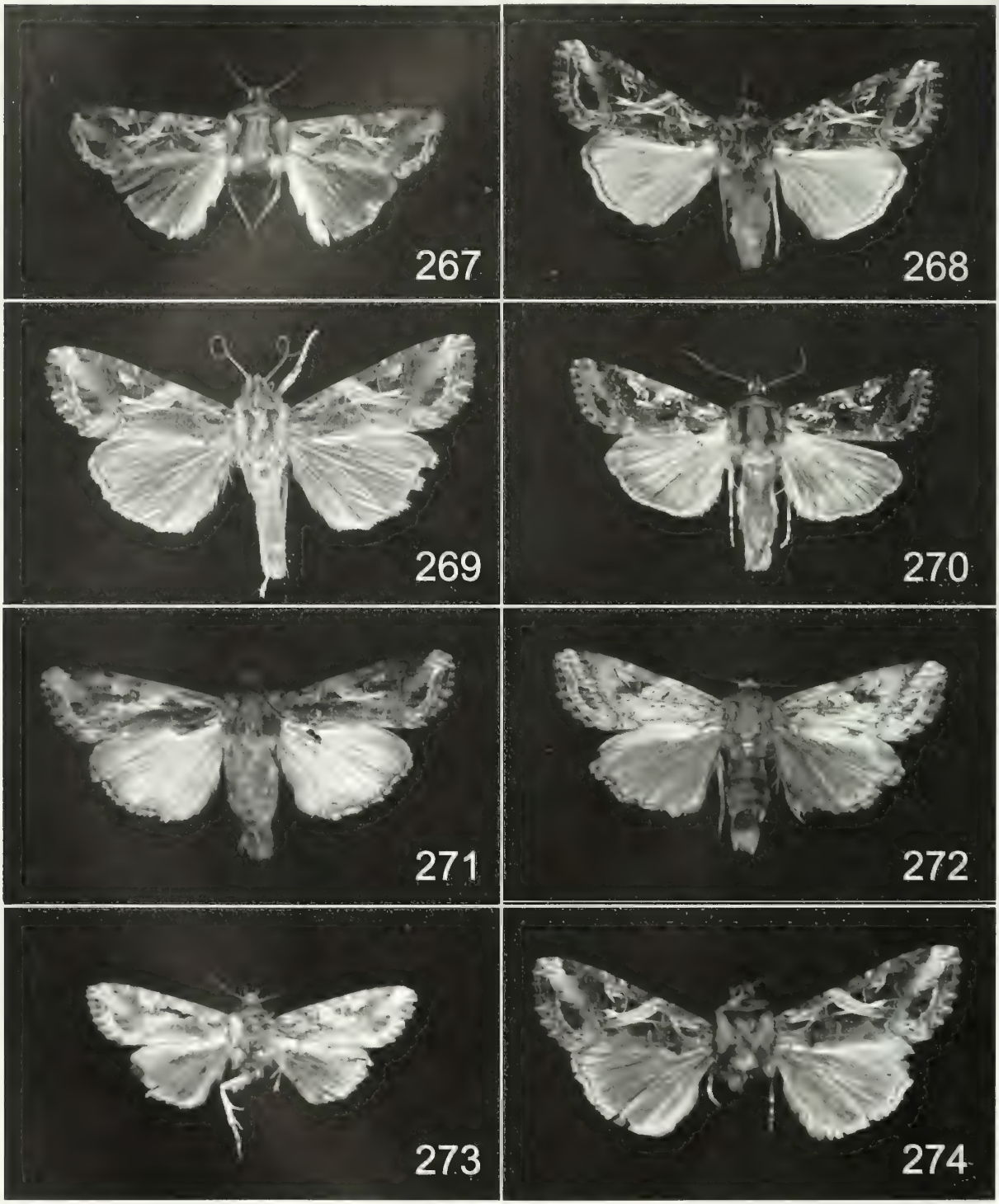
Figs. 249–252. *Spodoptera triturata* (Walker). 249, ♂, Liberia, USNMENT 65929 (USNM). 250, ♀ Lectotype, S. Leone, (BMNH). 251, ♂ Lectotype, *Celaena bisignata* Walker, synonym of *S. triturata*, S. Leone, (BMNH). 252, ♀ Holotype, *Laphygma gratiosa* Walker, synonym of *S. triturata*, S. Leone, (BMNH).



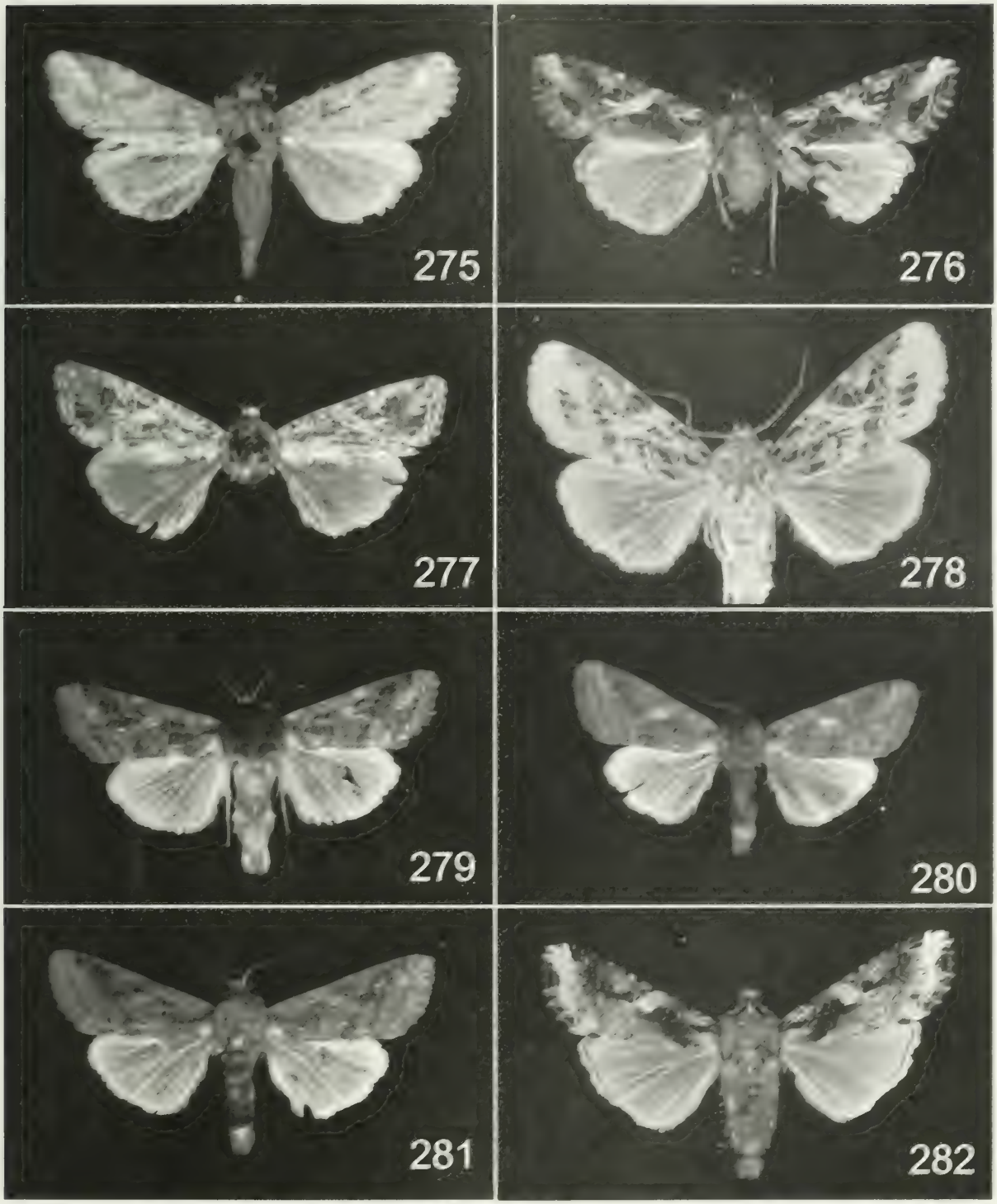
Figs. 253–258. *Spodoptera frugiperda* (J.E. Smith). 253, ♂ Neotype, Maryland, USNMENT 63639 (USNM). 254, ♀, Mississippi, USNMENT 60822 (USNM). 255, ♀ Lectotype, *Laphygma inepta* Walker, synonym of *S. frugiperda*, Brazil, (BMNH). 256, ♀ Lectotype, *Laphygma macra* Guenée, synonym of *S. frugiperda*, Colombia, (MNHN). 257, ♂ Holotype, *Prodenia plagiata* Walker, synonym of *S. frugiperda*, Jamaica, (BMNH). 258, ♀ Lectotype, *Prodenia signifera* Walker, synonym of *S. frugiperda*, U. S. America Georgia, (BMNH).



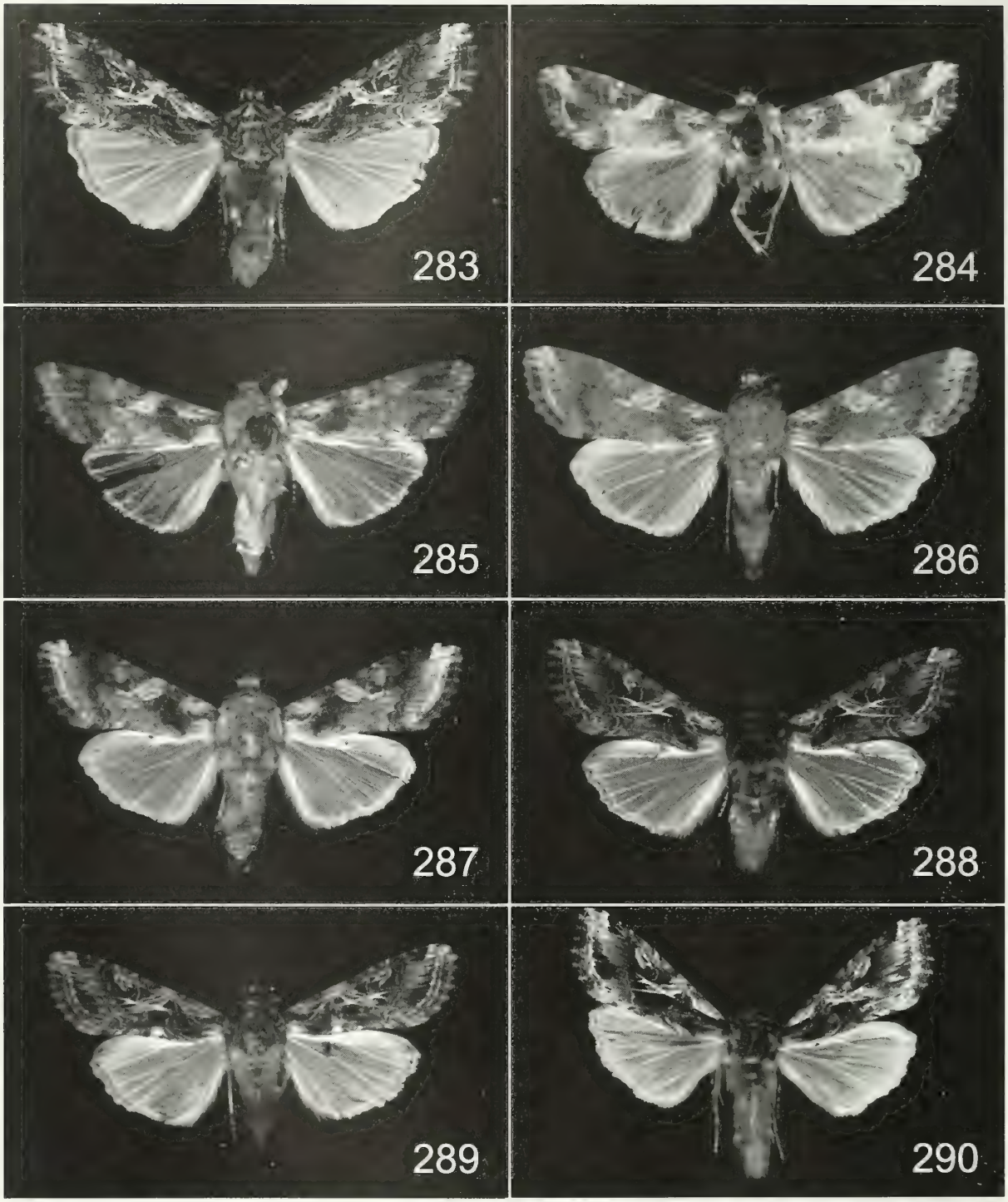
Figs. 259–266. *Spodoptera* spp. 259, ♀ Neotype, *S. dolichos* (Fabricius), Florida, USNMENT 62017 (USNM). 260, ♂ Neotype, *S. androgea* (Stoll), Dominica, USNMENT 61442 (USNM). 261, ♂, *S. androgea* (Stoll), Jamaica, USNMENT 61666 (USNM). 262, ♂ Holotype, *Prodenia rubrifusa* Hampson, synonym of *S. androgea*, Jamaica (BMNH). 263, ♂ Neotype, *S. littoralis* (Boisduval), Uganda, SPOD 0216 (USNM). 264, ♀, *S. littoralis*, Pakistan, USNMENT 65931 (USNM). 265, ♂, *S. littoralis*, Madagascar, (MNHN). 266, ♀, *S. littoralis*, Madagascar, (MNHN).



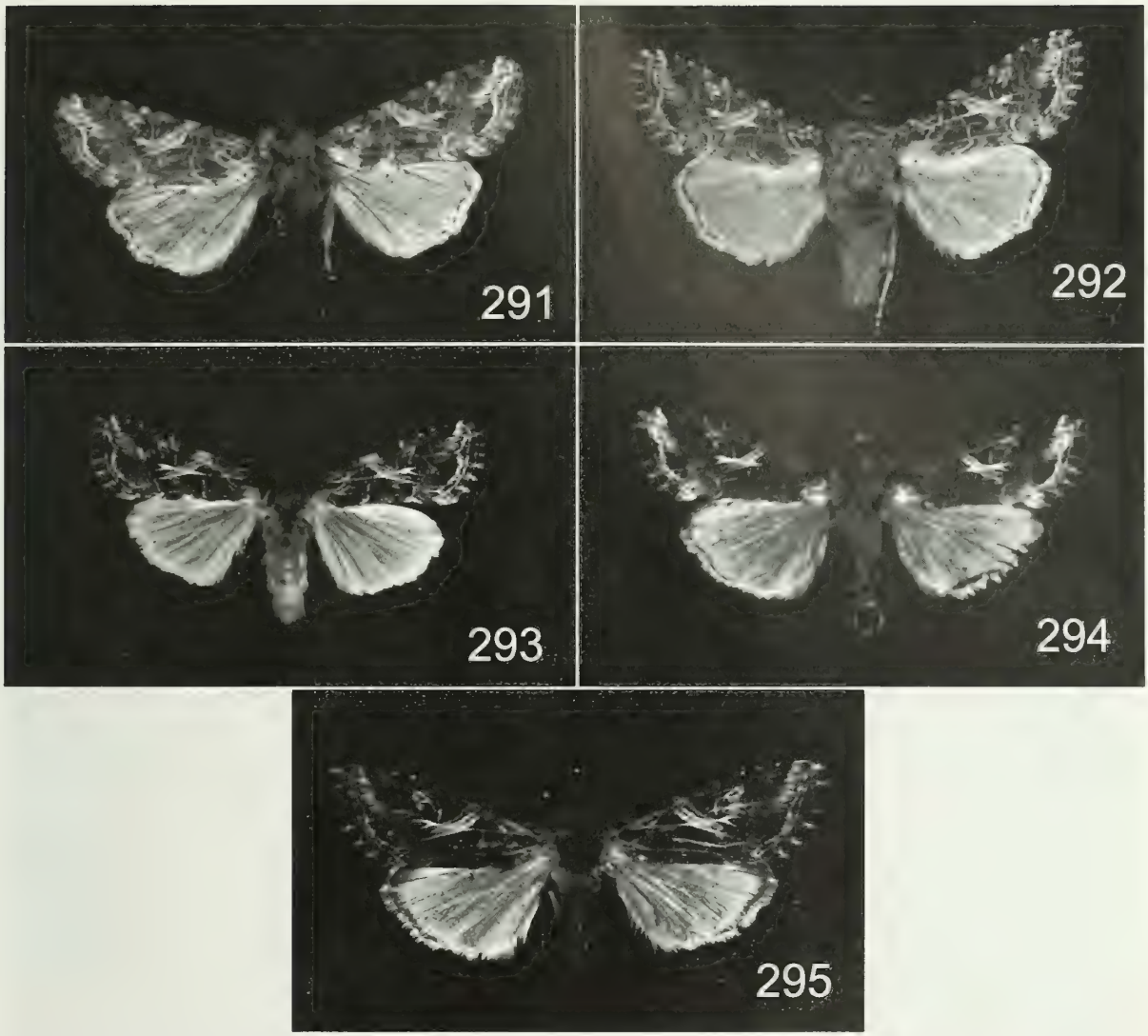
Figs. 267–274. *Spodoptera* spp. 267, ♂ Lectotype, *Prodenia testaceoides* Guenée, synonym of *S. littoralis*, Mauritius, (MNHN). 268, ♀, *S. litura* (Fabricius), New Caledonia, USNMENT 65934 (USNM). 269, ♂ Neotype, *S. litura* , India, SPOD 0360 (USNM). 270, ♂, *S. litura* , Christmas Island (BMNH). 271, ♂, *S. litura* , Pitcairn Island (BMNH). 272, ♀, *S. litura* , Henderson Island (BMNH). 273, ♂ Holotype, *Prodenia declinata* Walker, synonym of *S. litura*, N. India, (BMNH). 274, ♂ Lectotype, *Prodenia ciligera* Guenée, synonym of *S. litura*, Java [Indonesia], (BMNH).



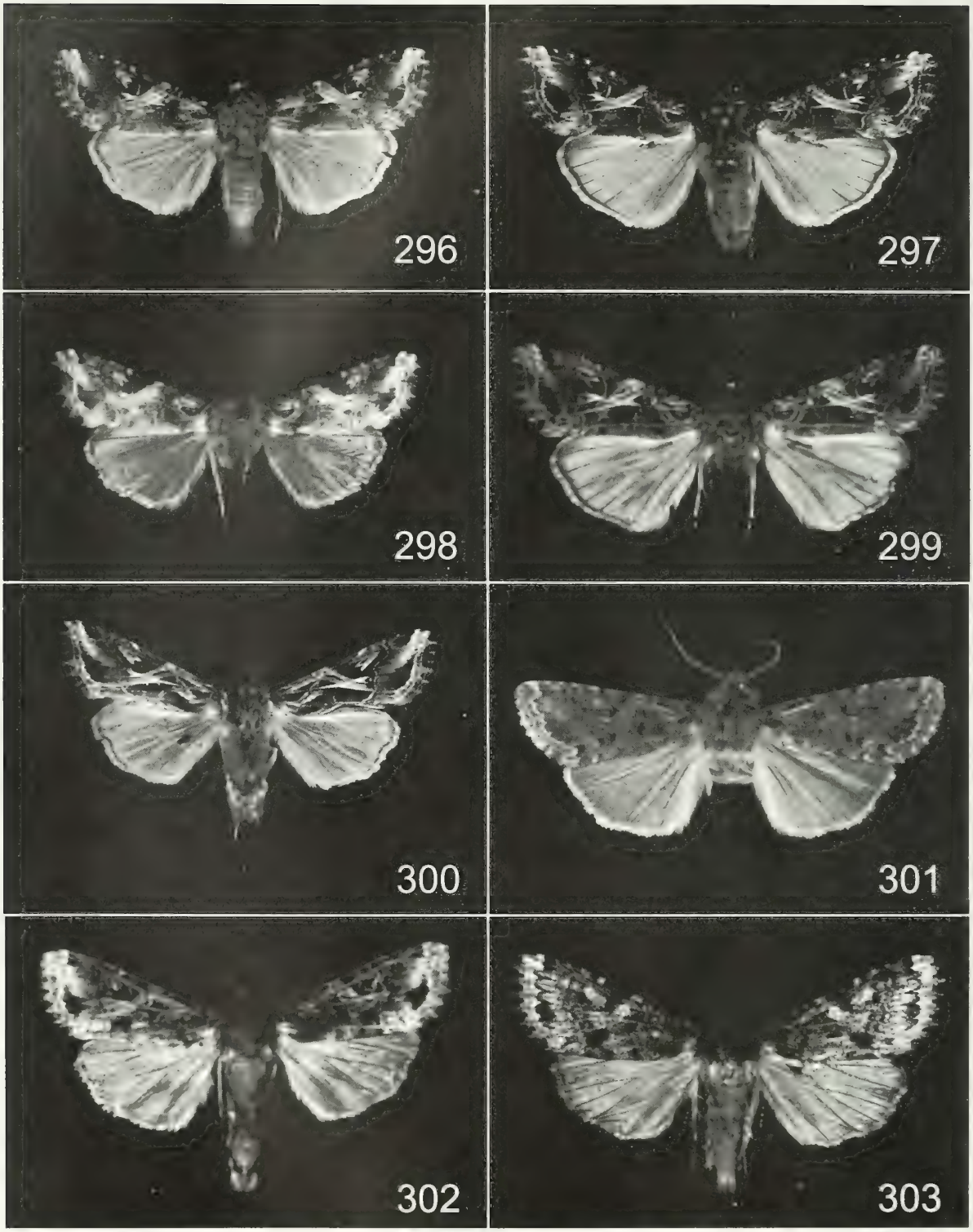
Figs. 275–282. *Spodoptera* spp. 275, ♀ Lectotype, *Prodenia evanescens* Butler, synonym of *S. litura*, S[outh] Pacific Caroline Is., (BMNH). 276, ♂ Lectotype, *Prodenia glaucistriga* Walker, synonym of *S. litura*, Canara, (BMNH). 277, ♀ Lectotype, *Prodenia subterminalis* Walker, synonym of *S. litura*, Punjab [India], (BMNH). 278, ♂ Neotype *S. picta* (Guérin-Méneville), Australia, SPOD 1402 (USNM). 279, ♂, *S. evanida* Schaus, French Guiana, USNMENT 65936 (USNM). 280, ♂, *S. evanida*, French Guiana, (BMNH). 281, ♀, *S. evanida*, French Guiana, (BMNH). 282, ♂, *S. latifascia* (Walker), U.S.A. Florida, USNMENT 65941 (USNM).



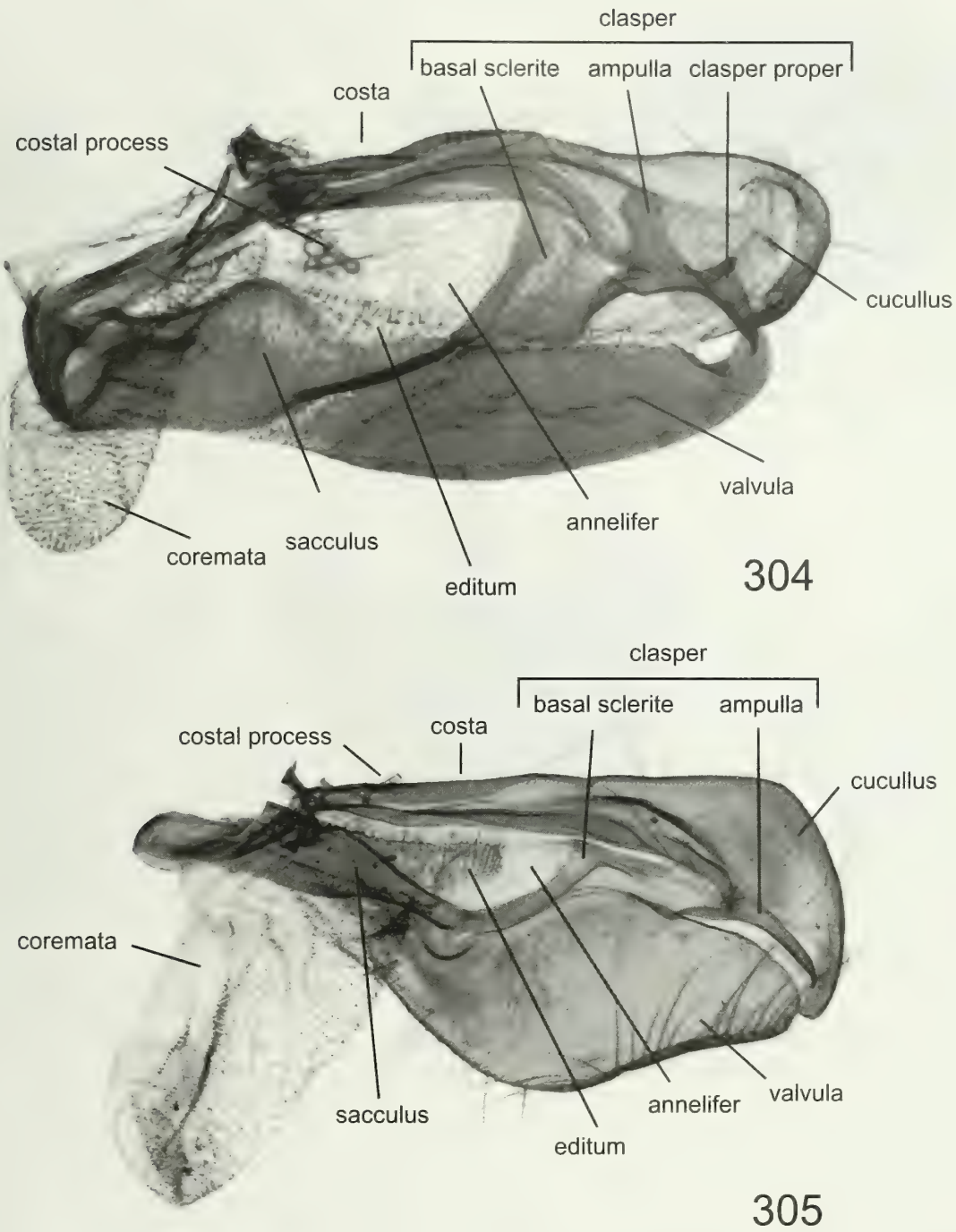
Figs. 283–290. *Spodoptera* spp. 283, ♀, *S. latifascia*, U.S.A. Florida, USNMENT 65942 (USNM). 284, ♂ Lectotype, *Prodenia variolosa* Walker, synonym of *S. latifascia*, St. Domingo [Dominican Republic], (BMNH). 285, ♂, *S. cosmiodes* (Walker), Para [Brazil], (BMNH). 286, ♂, *S. cosmiodes*, Brazil, USNMENT 65937 (USNM). 287, ♀, *S. cosmiodes*, French Guiana, USNMENT 65938 (USNM). 288, ♀, *S. cosmiodes*, French Guiana, USNMENT 65939 (USNM). 289, ♀, *S. cosmiodes*, Venezuela, USNMENT 65940 (USNM). 290, ♀, *S. descoinsi* Lalanne-Cassou and Silvain, French Guiana, USNMENT 61984 (USNM).



Figs. 291–295. *Spodoptera* spp. 291, ♂ Lectotype, *S. praefica* (Grote), U.S.A. California, (BMNH). 292, ♂, *S. praefica*, U.S.A. Utah, USNMENT 65943 (USNM). 293, ♀, *S. marima* (Schaus), Venezuela, USNMENT 65945 (USNM). 294, ♂, *S. marima*, Peru (BMNH). 295, ♀, *S. marima*, Peru (BMNH).



Figs. 296–303. *Spodoptera* spp. 296, ♂, *S. ornithogalli* (Guenée), U.S.A. Texas, USNMENT 65946 (USNM). 297, ♀, *S. ornithogalli*, U.S.A. Texas, USNMENT 65947 (USNM). 298, ♂ Lectotype, *Prodenia flavimedia* Harvey, synonym of *S. ornithogalli*, U.S. America, (BMNH). 299, ♀ Lectotype, *Prodenia lineatella* Harvey, synonym of *S. ornithogalli*, U.S. America, (BMNH). 300, ♀, *S. pulchella* (Herrich-Schäffer), U.S.A. Florida, USNMENT 65944 (USNM). 301, ♂ Holotype, *S. roseae* (Schaus). 302, ♂, *S. roseae*, Galapagos, (BMNH). 303, ♀, *S. roseae*, Galapagos, (BMNH).



Figs. 304–305. Male genitalia illustrating parts discussed in text. 304, Valve of *S. albula*. 305, Valve of *S. frugiperda*.

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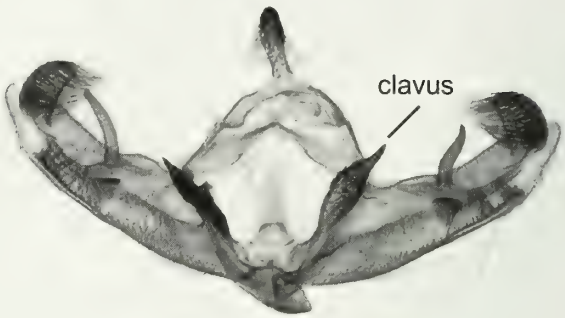

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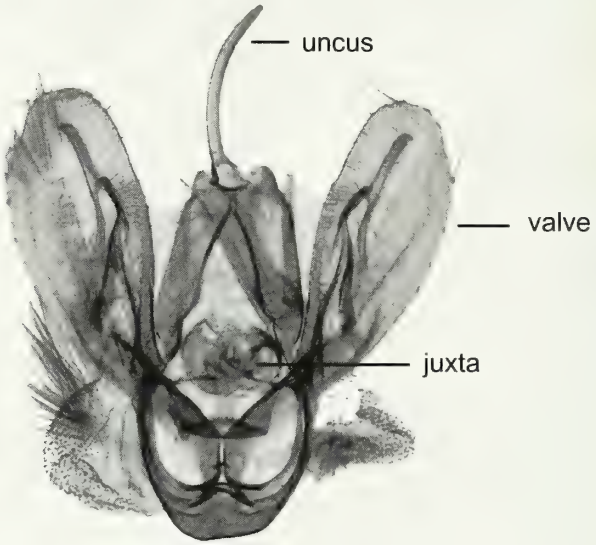

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Figs. 306–308. Male genitalia. 306, *Elaphria grata*, used as an outgroup for phylogenetic analysis. 307, *Galgula partita*, used as an outgroup for phylogenetic analysis. 308, *S. exigua*.

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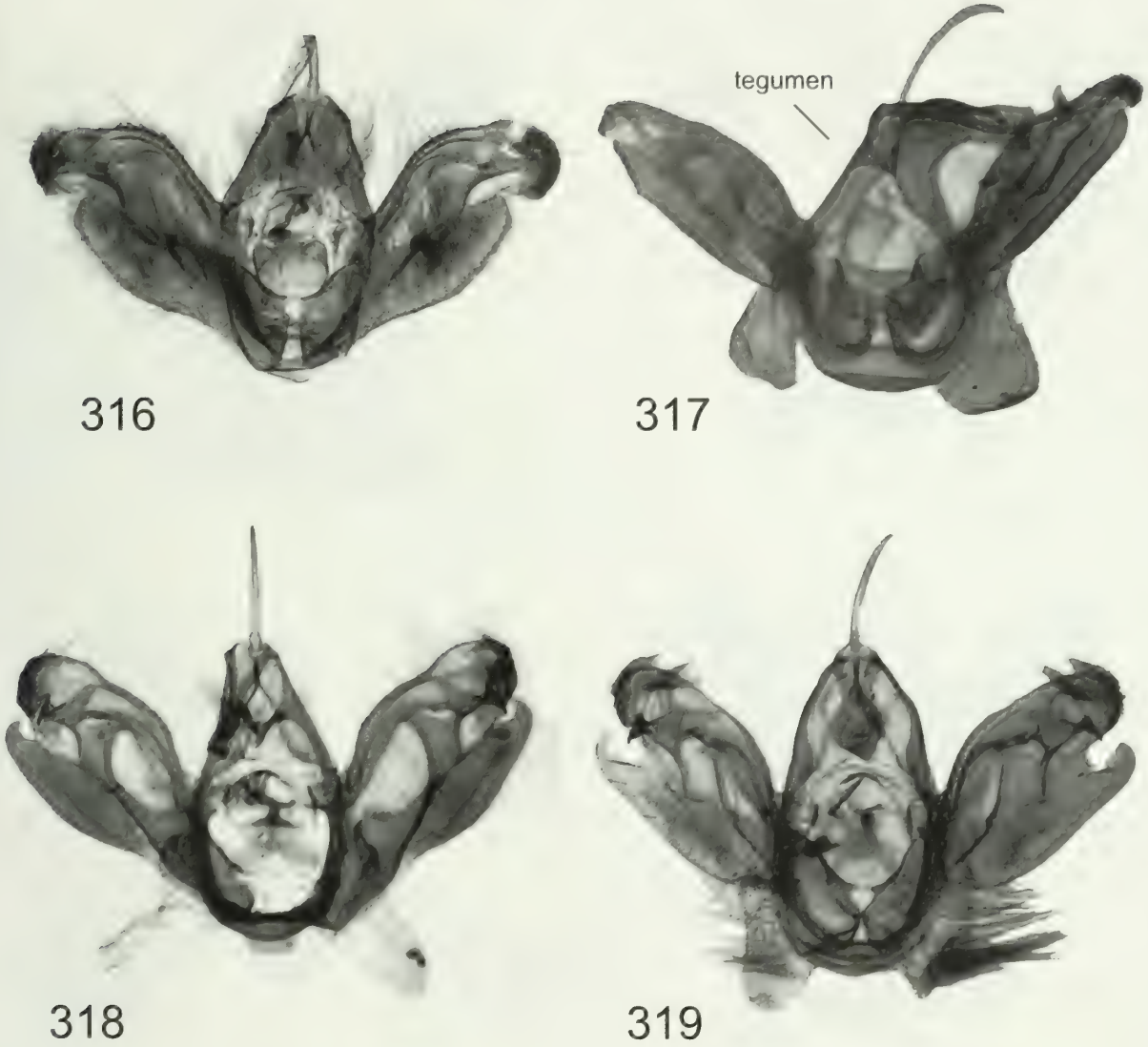
Figs. 309–311. *S. cilium* clade male genitalia. 309, *S. cilium*. 310, *S. depravata*. 311, *S. pecten*.

Figs. 312–315. *S. umbraculata* clade male genitalia. 312, *S. umbraculata*. 313, *S. pectinicornis*. 314, *S. apertura*. 315, *S. malagasy*.



Figs. 316–319. Clade 21 male genitalia. 316, *S. compta*. 317, *S. eridania*. 318, *S. albula*. 319, *S. ochrea*.

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Figs. 320–323. *S. exempta* clade and *S. frugiperda* male genitalia. 320, *S. exempta.* 321, *S. mauritia.* 322, *S.triturata.* 323, *S. frugiperda.*

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Figs. 324–328. *S. dolichos* and *S. littoralis* clades male genitalia. 324, *S. dolichos*. 325, *S. androgea*. 326, *S. littoralis*. 327, *S. litura*. 328, *S. picta*.

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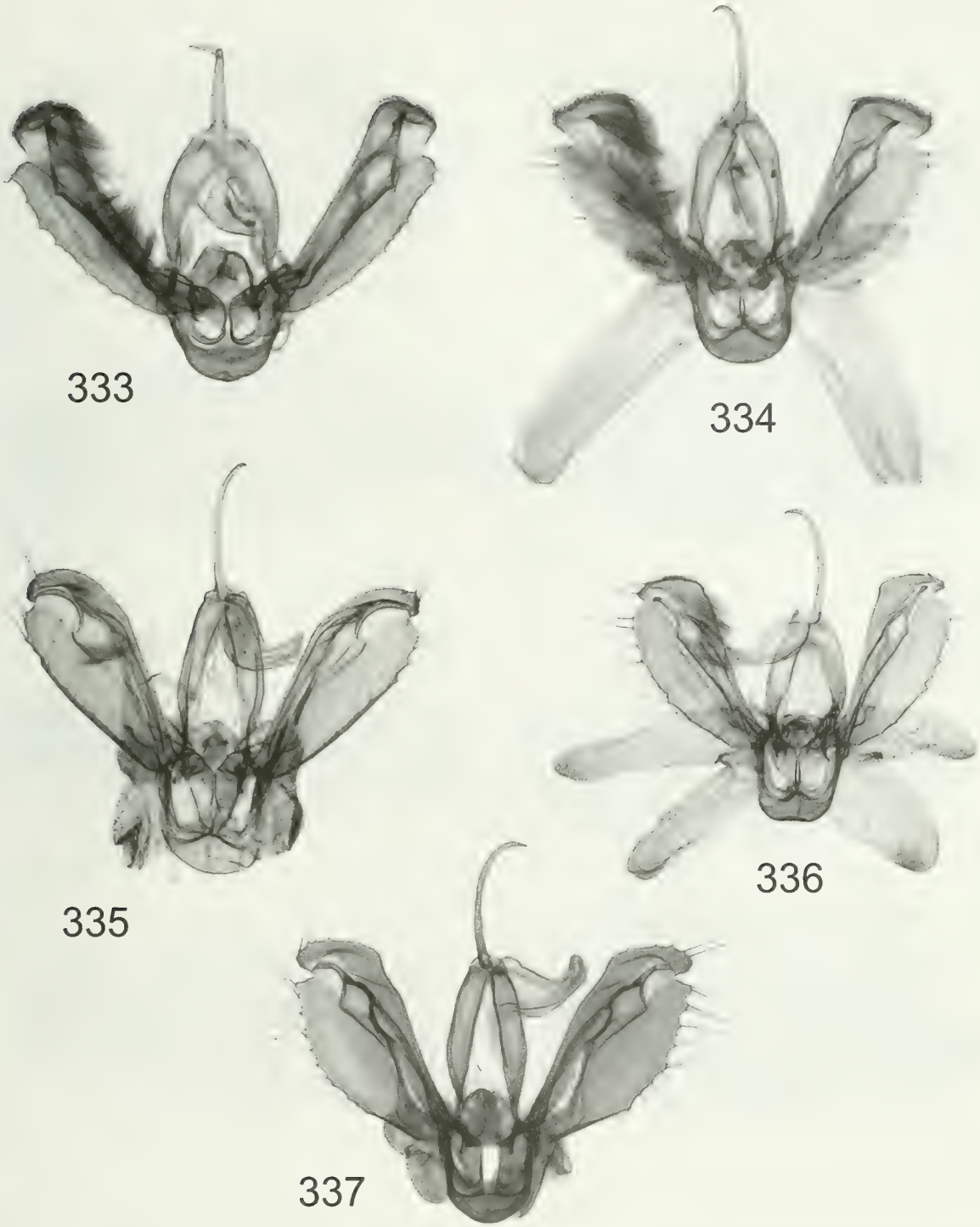
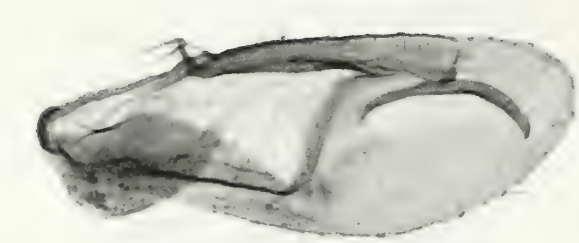
Figs. 329–332. *S. evanida* clade male genitalia. 329, *S. evanida*. 330, *S. latifascia*. 331, *S. cosmiodes*. 332, *S. descoinsi*.



Figs. 333–337. *S. praefica* clade male genitalia. 333, *S. praefica*. 334, *S. marima*. 335, *S. ornithogalli*. 336, *S. pulchella*. 337, *S. roseae*.



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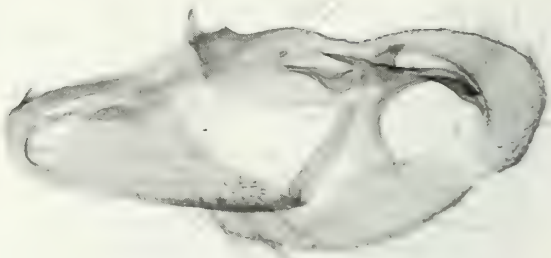

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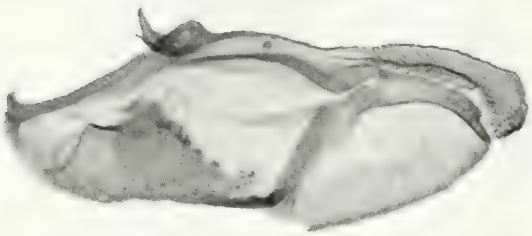

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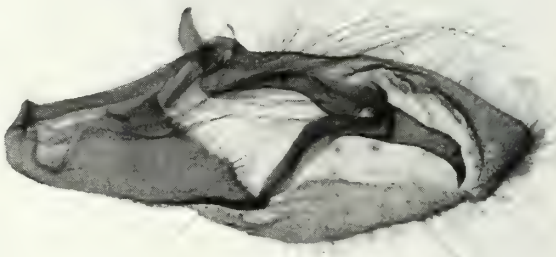

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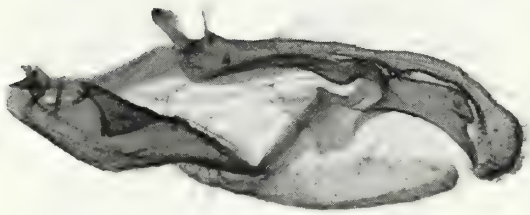

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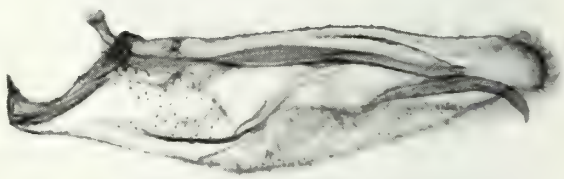

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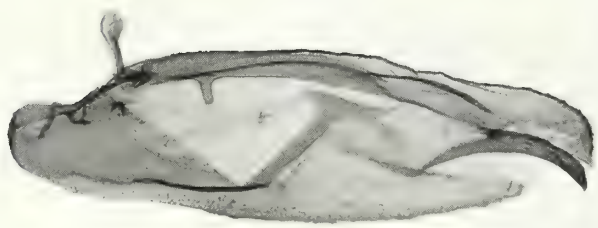

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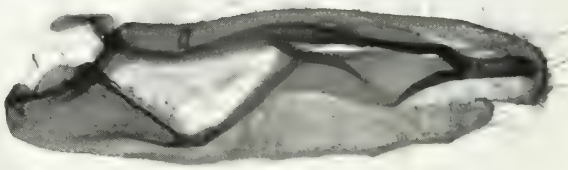

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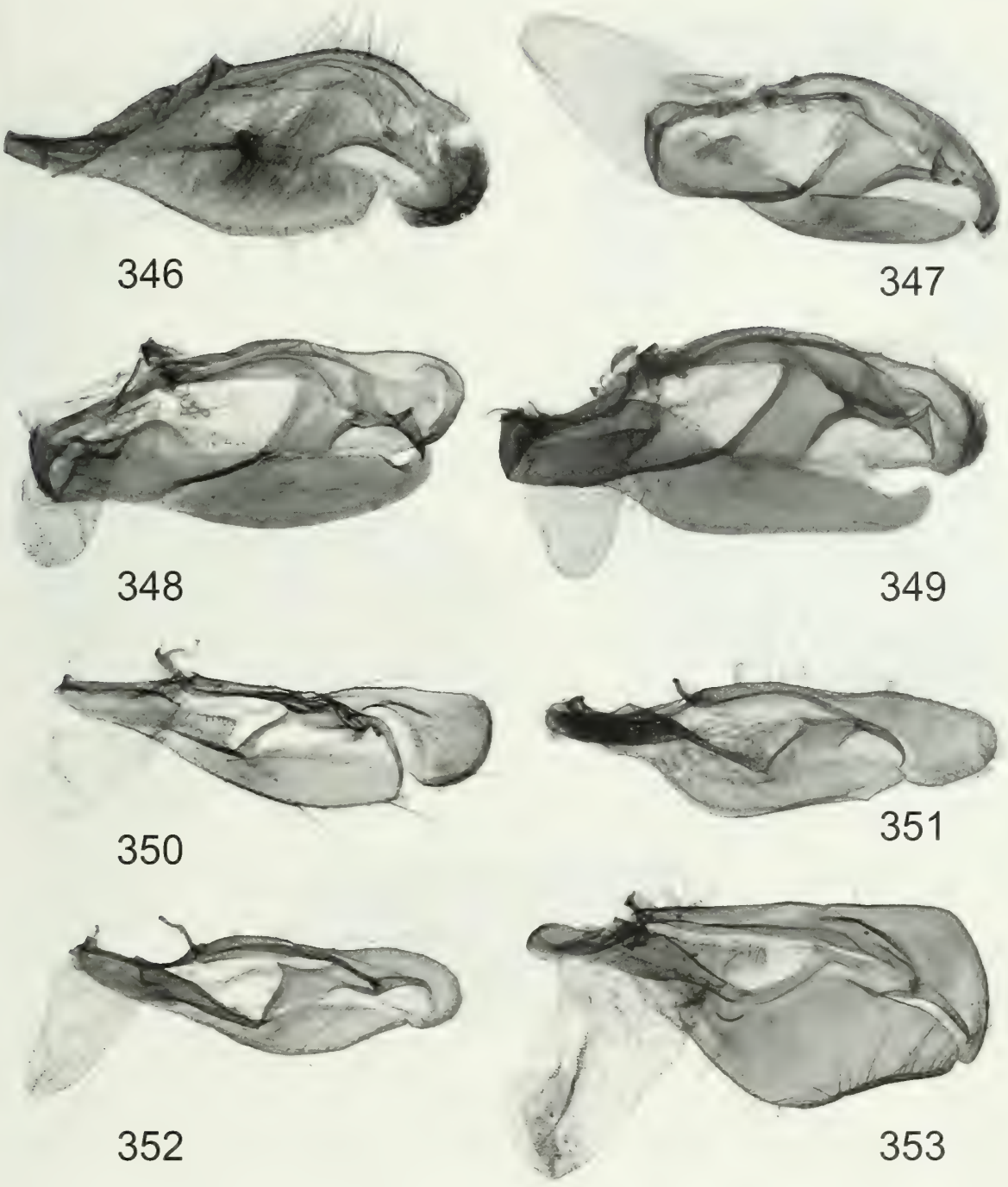
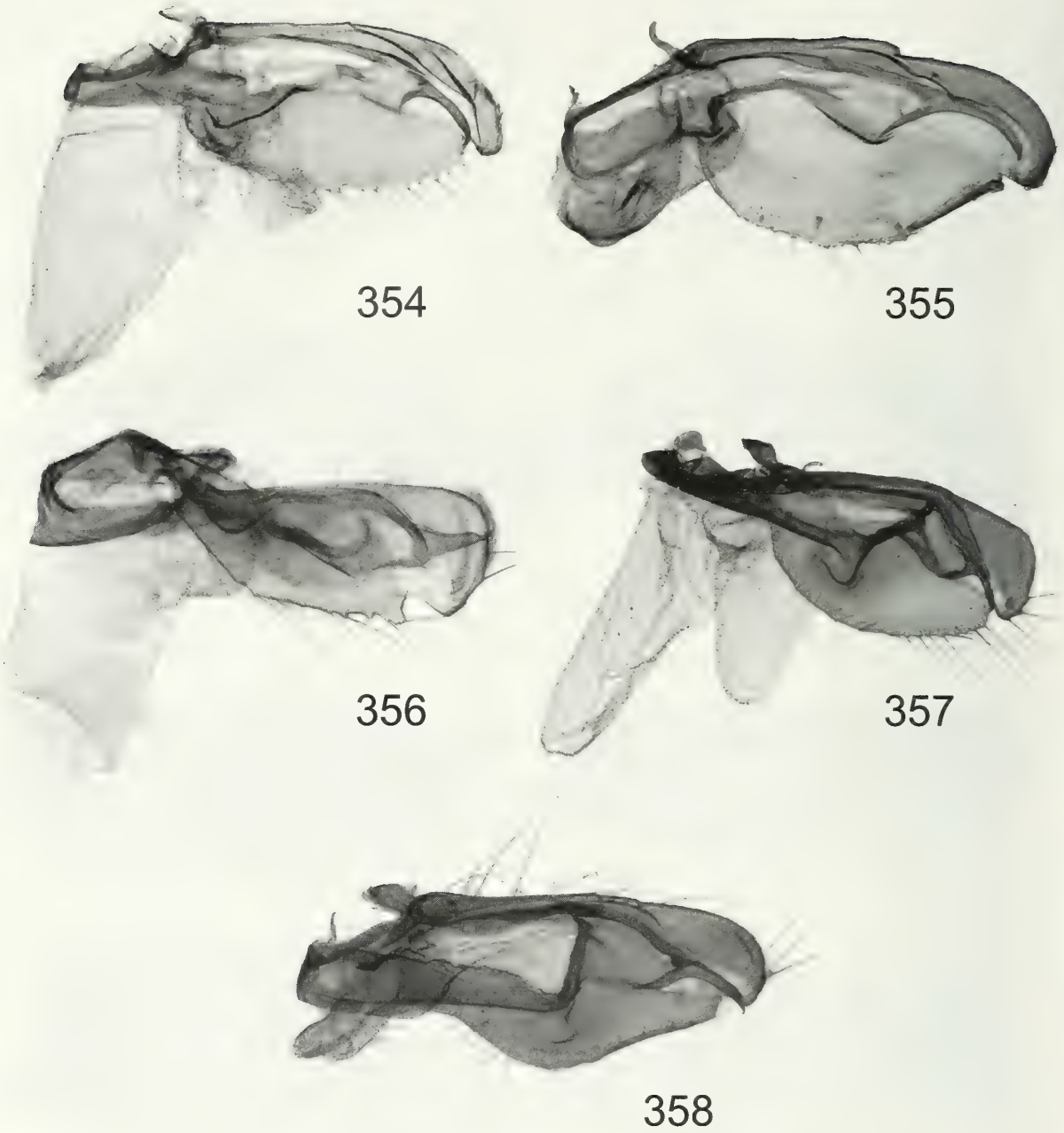
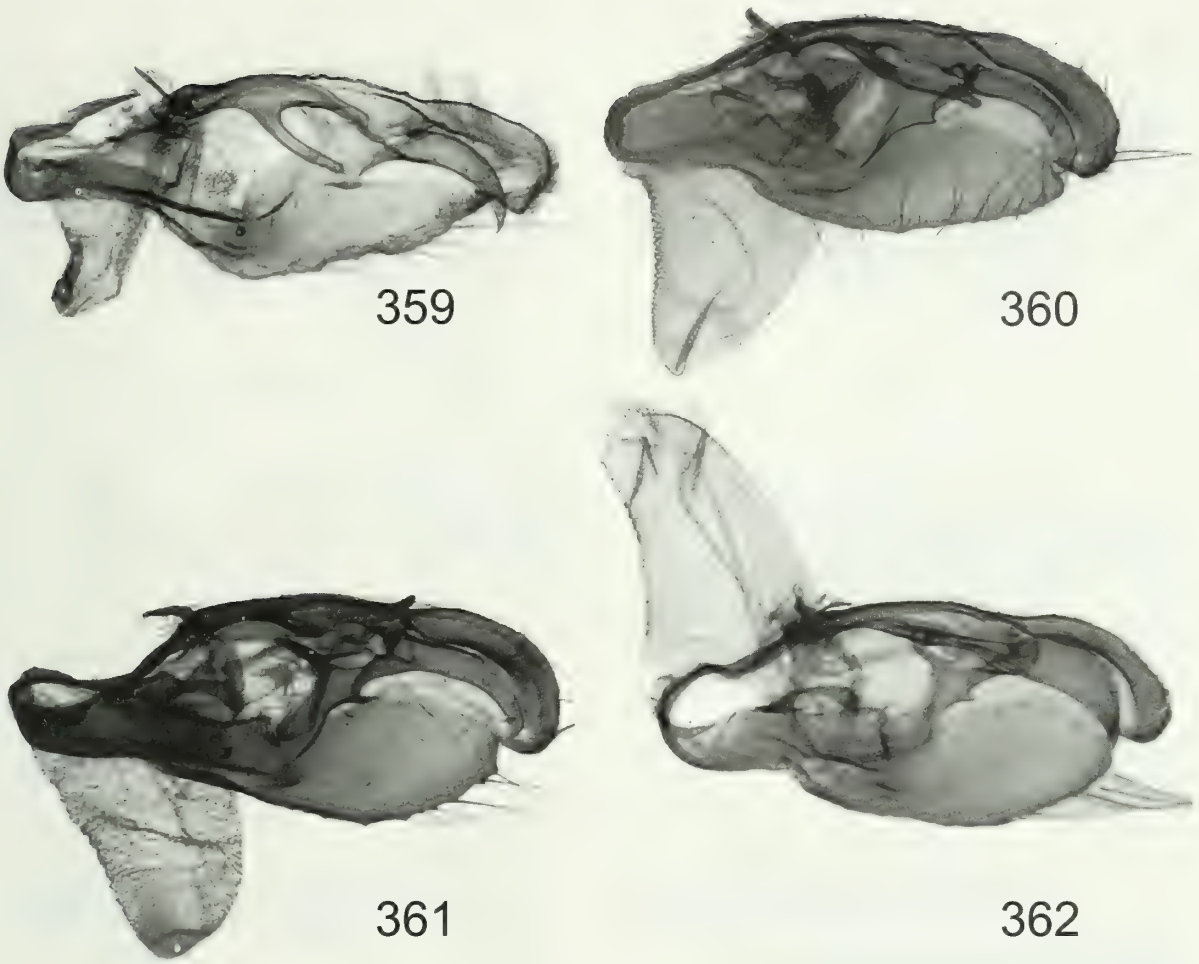
Figs. 338–345. *Spodoptera* species male valves. 338, *S. exigua*. 339, *S. cilium*. 340, *S. depravata*. 341, *S. pecten*. 342, *S. umbraculata*. 343, *S. pectinicornis*. 344, *S. apertura*. 345, *S. malagasy*.



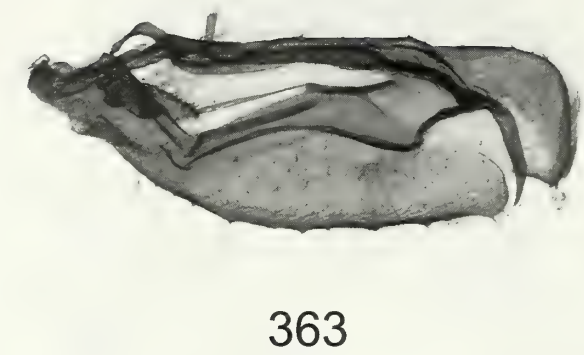
Figs. 346–353. Clade 21 and *S. exempta* clades and *S. frugiperda* male valves. 346, *S. compta*. 347, *S. eridania*. 348, *S. albula*. 349, *S. ochrea*. 350, *S. exempta*. 351, *S. mauritia*. 352, *S.triturata*. 353, *S. frugiperda*.



Figs. 354–358. *S. dolichos* and *S. littoralis* clades male valves. 354, *S. dolichos*. 355, *S. androgea*. 356, *S. littoralis*. 357, *S. litura*. 358, *S. picta*.



Figs. 359–362. *S. evanida* clade male valves. 359, *S. evanida*. 360, *S. latifascia*. 361, *S. cosmiodes*. 362, *S. descoinsi*.



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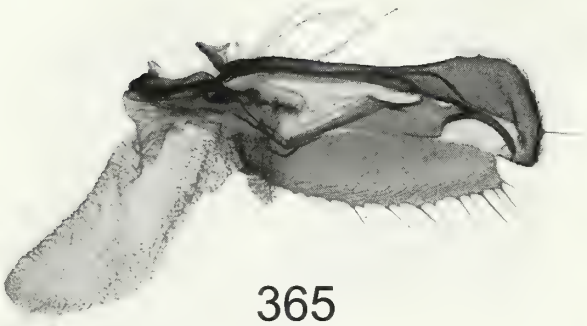

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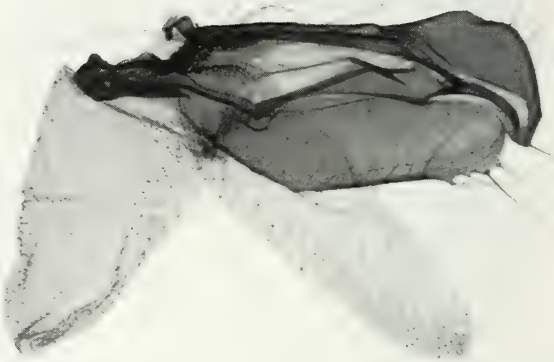

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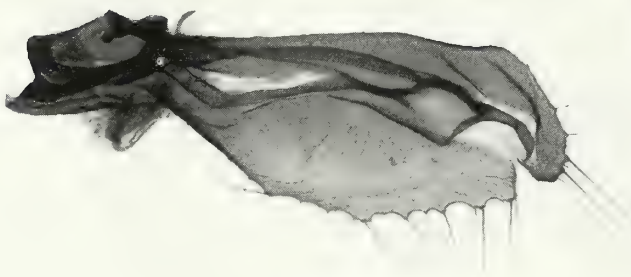

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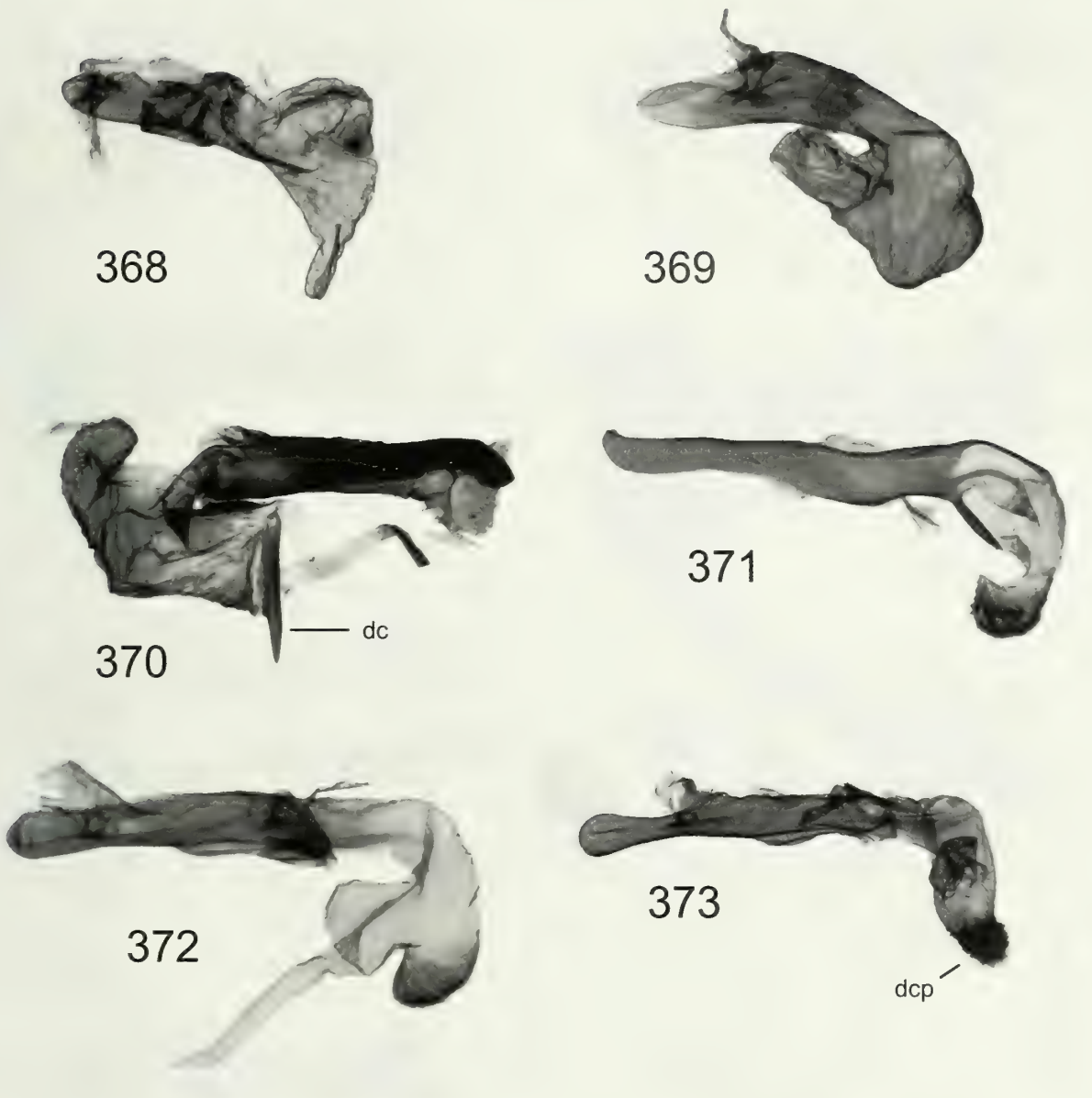
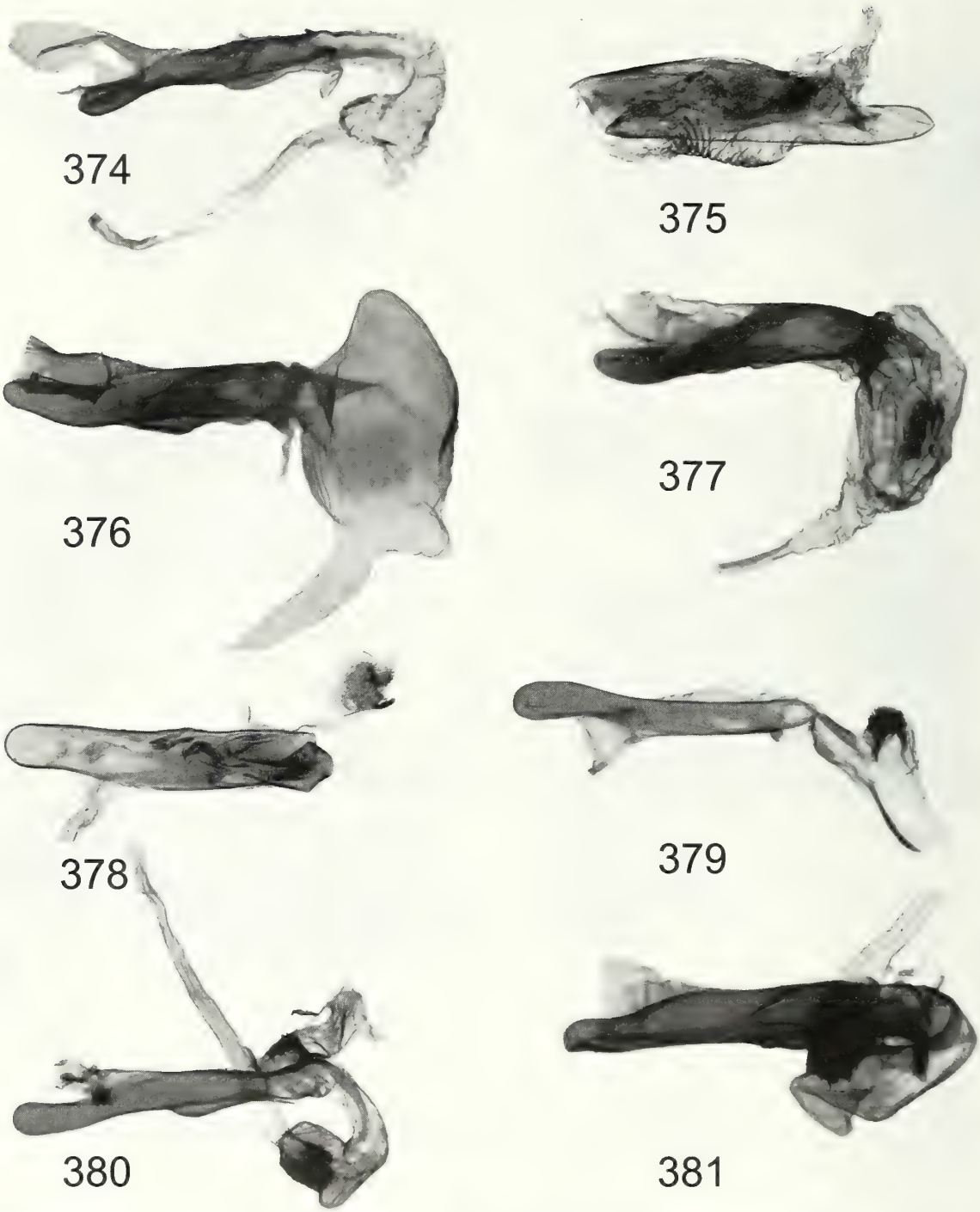
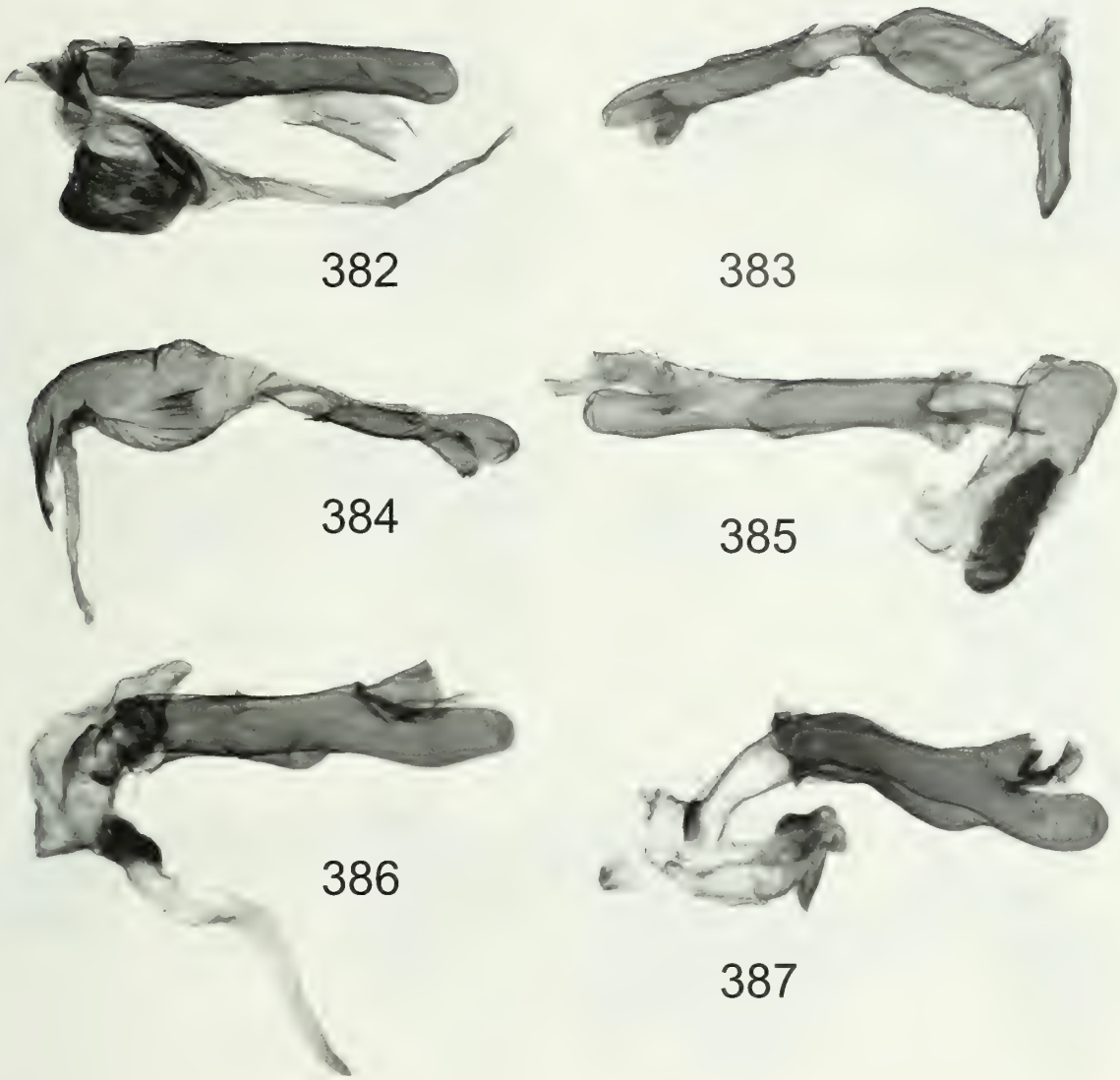
Figs. 363–367. *S. praefica* clade male genitalia. 363, *S. praefica*. 364, *S. marima*. 365, *S. ornithogalli*. 366, *S. pulchella*. 367, *S. roseae*.



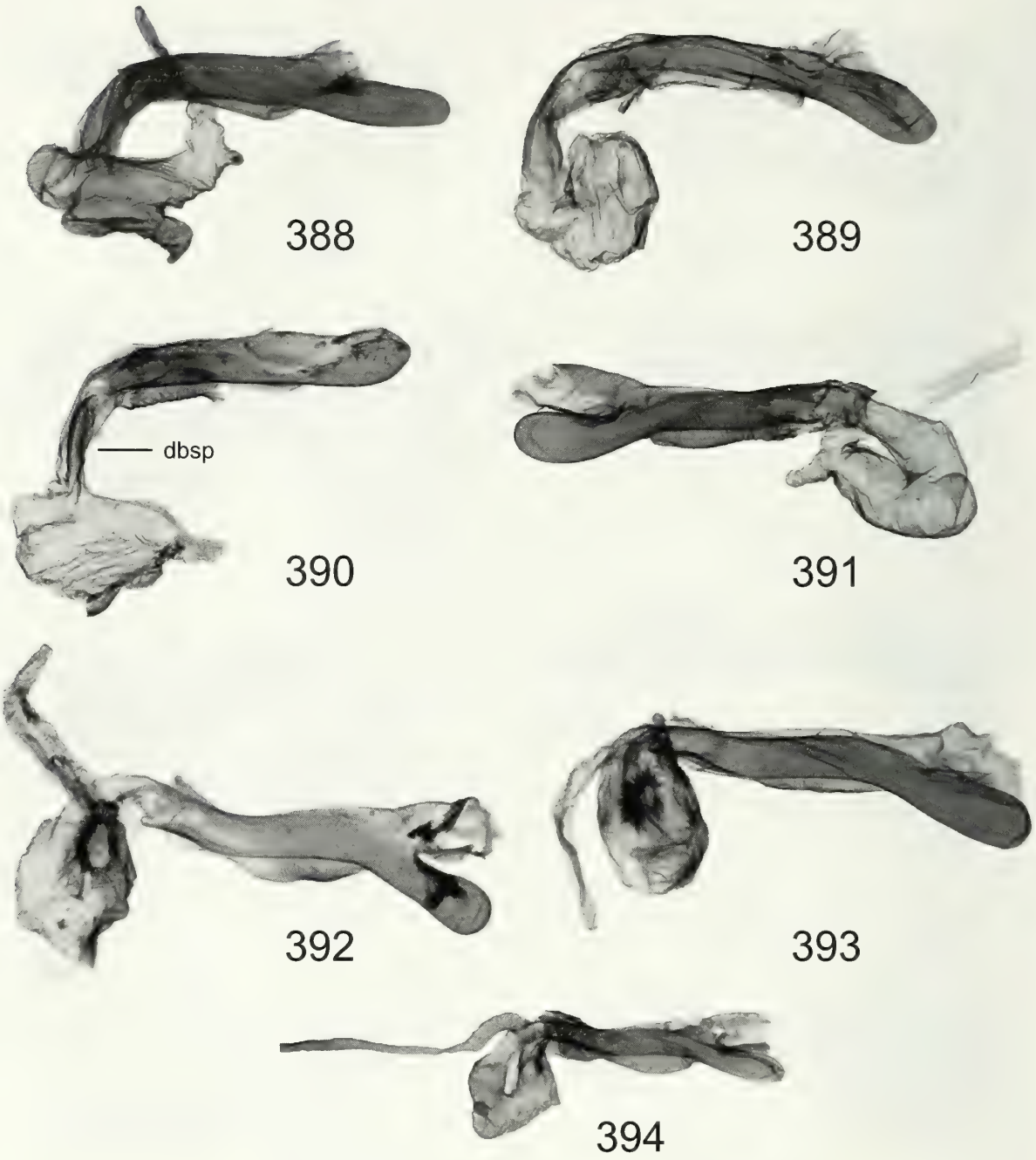
Figs. 368–373. Male aedoeagi of outgroups, *S. exigua* and *S. cilium* clade. 368, *Galgula partita*. 369, *Elaphria grata*. 370, *S. exigua* . 371, *S. cilium*. 372, *S. depravata*. 373, *S. pecten*. Abbreviations: dc, distal cornutus; dcp, distal cornutal patch.



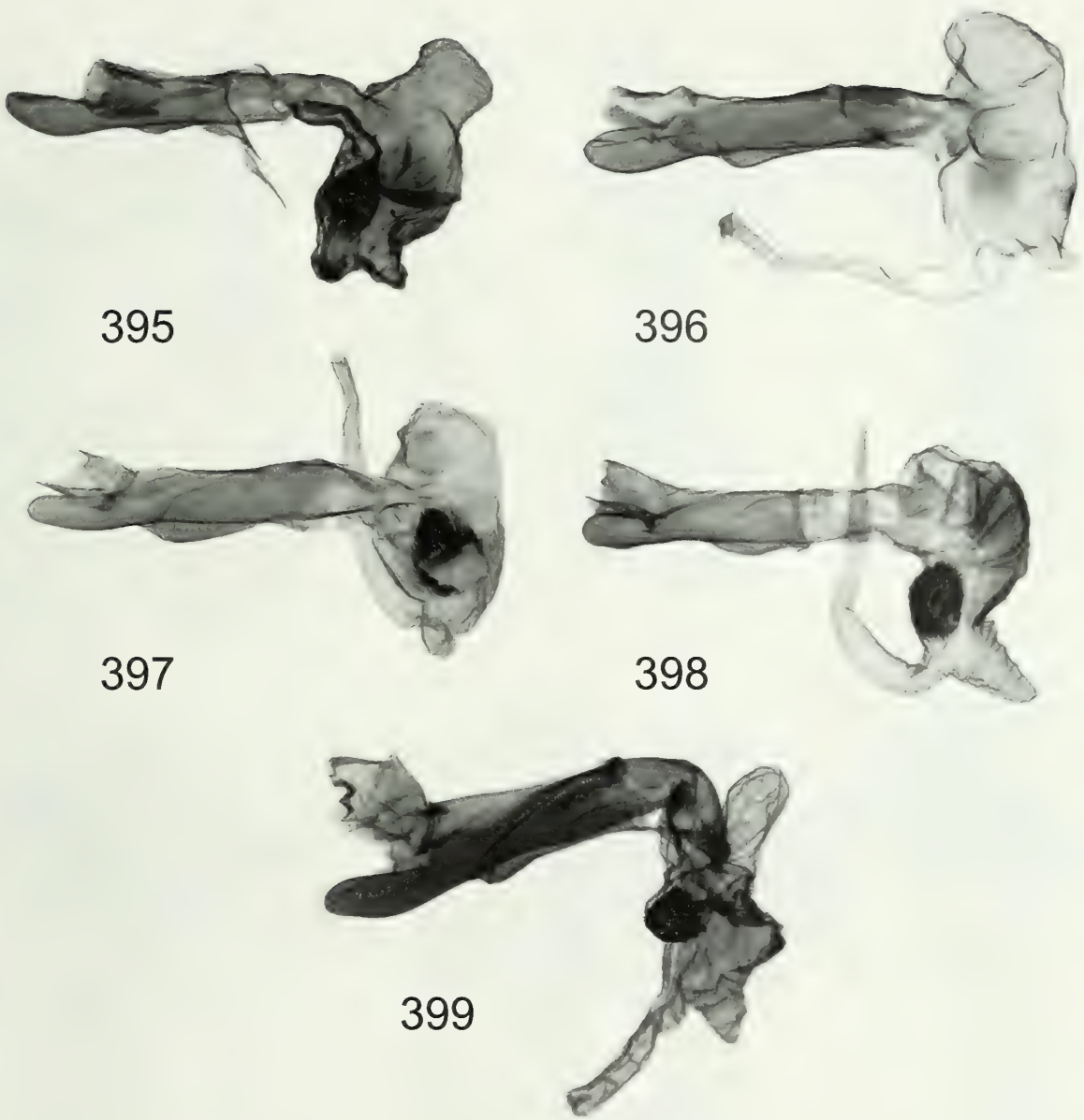
Figs. 374–381. *S. umbraculata* clade and Clade 21 male aedoeagi. 374, *S. umbraculata*. 375, *S. pectinicornis*. 376, *S. apertura*. 377, *S. malagasy*. 378, *S. compta*. 379, *S. eridania*. 380, *S. albula*. 381, *S. ochrea*.



Figs. 382–387. *S. exempta, S. frugiperda* , and *S. dolichos* clades male aedoeagi. 382, *S. exempta.* 383, *S. mauritia.* 384, *S.triturata.* 385, *S. frugiperda.* 386, *S. dolichos.* 387, *S. androgea.*



Figs. 388–394. *S. littoralis* and *S. evanida* clades male aedoeagi. 388, *S. littoralis*. 389, *S. litura*. 390, *S. picta*. 391, *S. evanida*. 392, *S. latifascia*. 393, *S. cosmiodes*. 394, *S. descoinsi*. Abbreviations: dbsp, dorso-basal sclerotized patch.



Figs. 395–399. *S. praefica* clade male aedoeagi. 395, *S. praefica*. 396, *S. marima*. 397, *S. ornithogalli*. 398, *S. pulchella*. 399, *S. roseae*.

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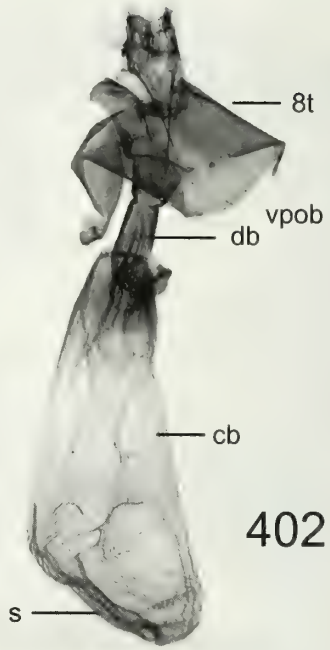

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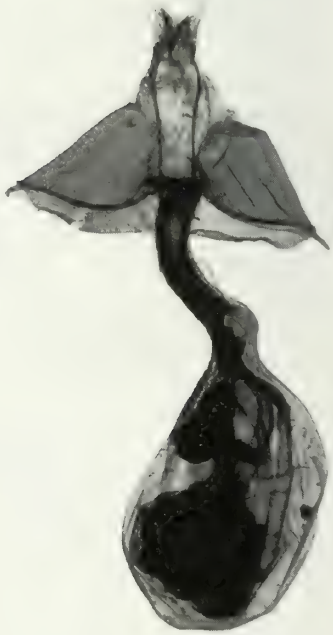

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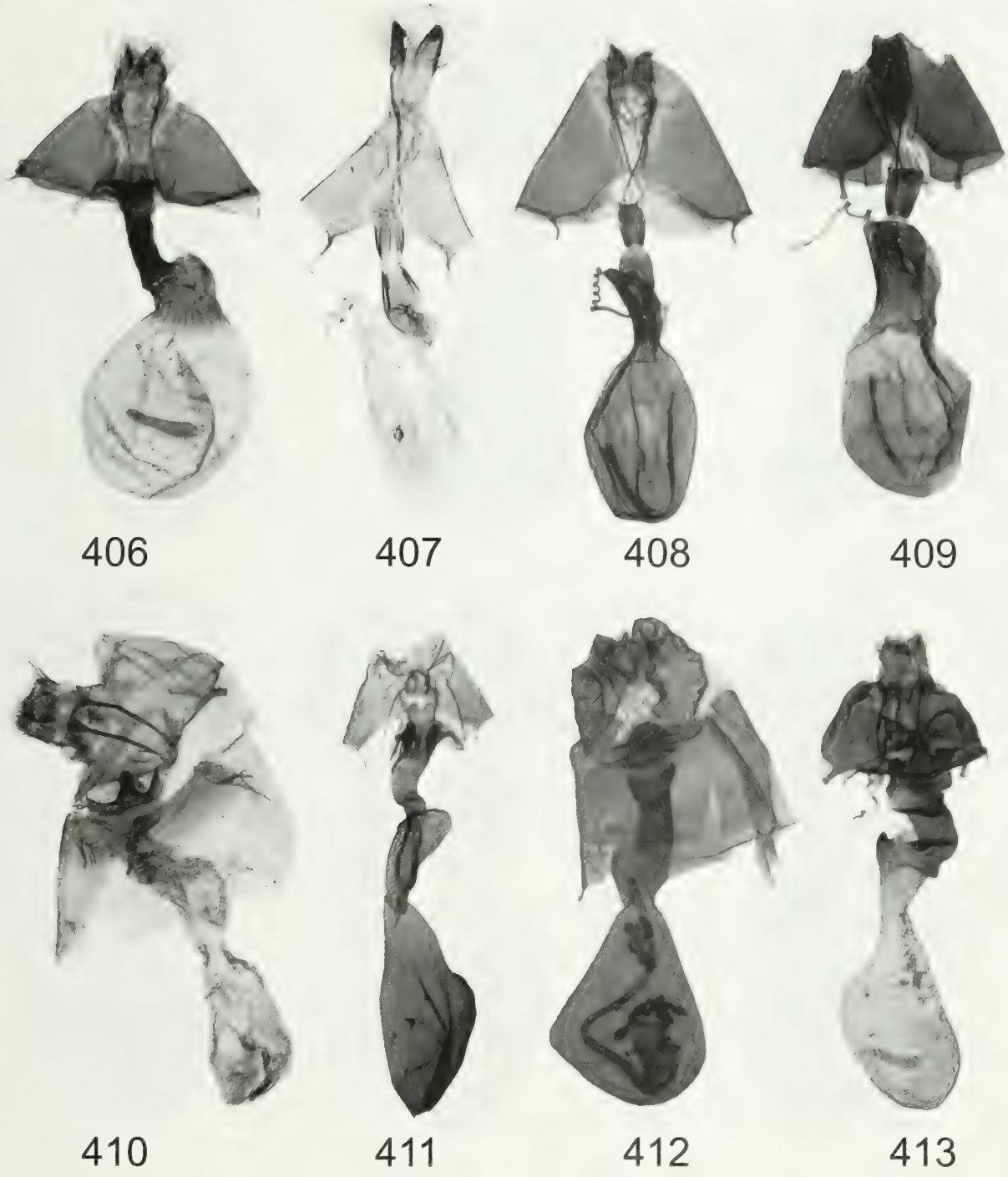
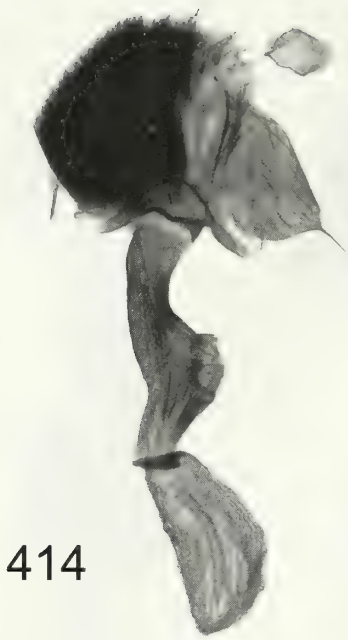
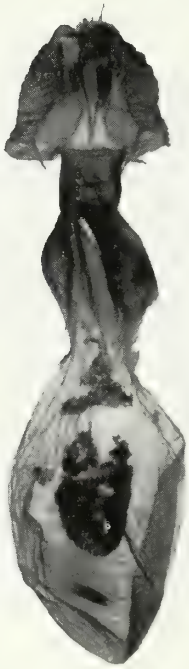
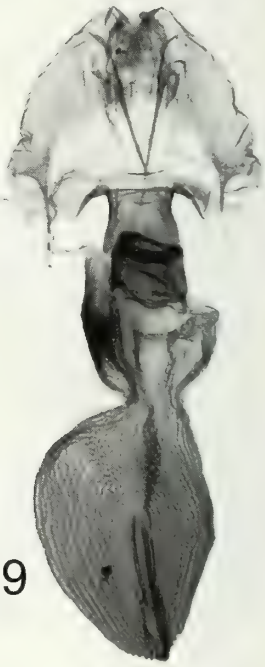
Figs. 400–405. Female genitalia of outgroups and *S. exigua* and *S. cilium* clade. 400, *Elaphria grata*. 401, *Galgula partita*. 402, *S. exigua*. 403, *S. cilium*. 404, *S. depravata*. 405, *S. pecten*. Abbreviations: 8t, eighth tergite; cb, corpus bursae; db, ductus bursae; s, signum; vpob, ventral plate of ostium bursa.



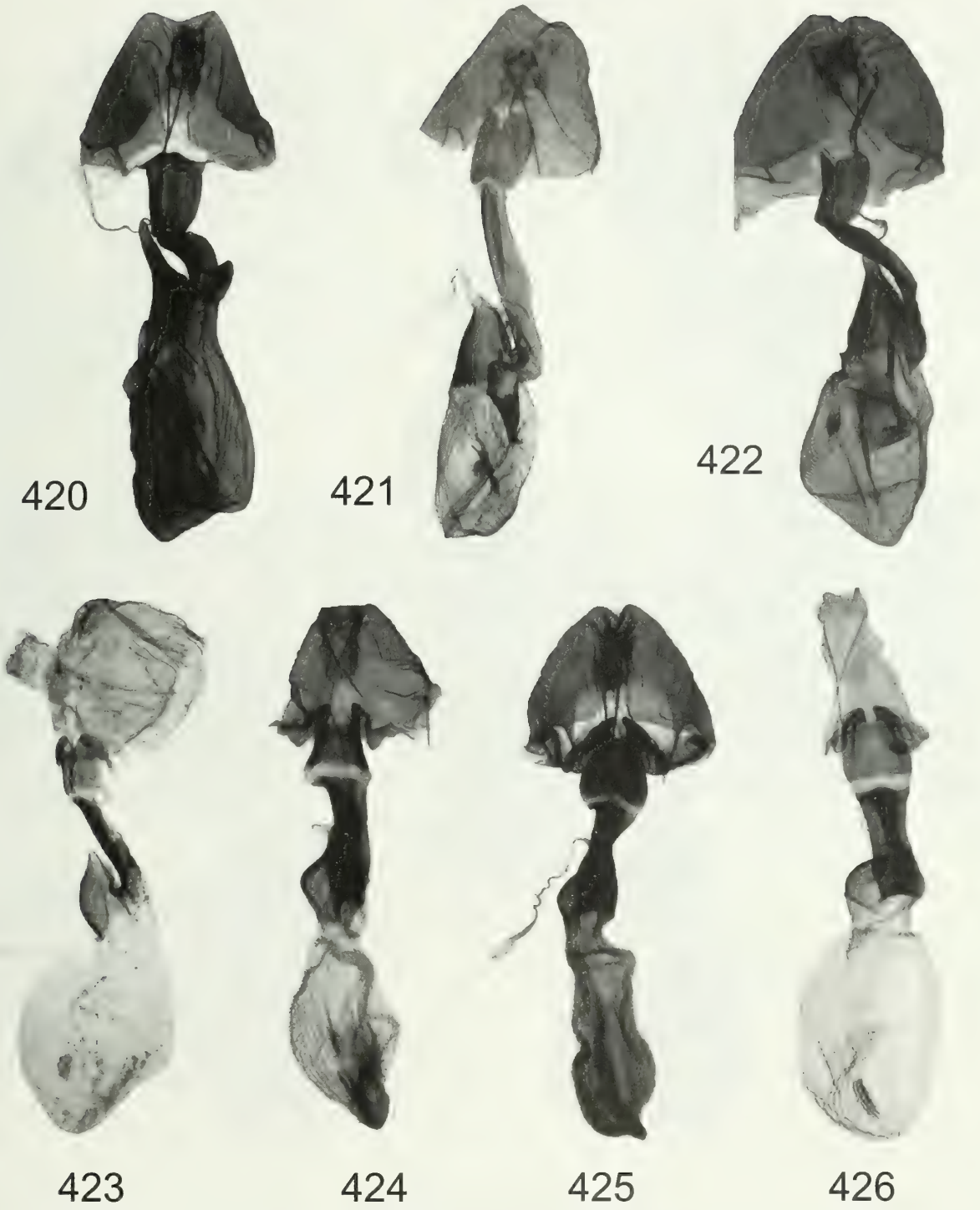
Figs. 406–413. Female genitalia of *S. umbraculata* clade and Clade 21female genitalia. 406, *S. umbraculata*. 407, *S. pectinicornis*. 408, *S. apertura*. 409, *S. malagasy*. 410, *S. compta*. 411, *S. eridania*. 412, *S. albula*. 413, *S. ochrea*.







Figs. 414–419. Female genitalia of *S. exempta* clade, *S. frugiperda,* and *S. dolichos* clade female genitalia. 414, *S. exempta.* 415, *S. mauritia.* 416, *S.triturata.* 417, *S. frugiperda.* 418, *S. dolichos.* 419, *S. androgea.*



Figs. 420–426. Female genitalia of *S. littoralis* and *S. evanida* clades female genitalia. 420, *S. littoralis.* 421, *S. litura.* 422, *S. picta.* 423, *S. evanida.* 424, *S. latifascia.* 425, *S. cosmiodes.* 426, *S. descoinsi.*

Figs. 427–431. Female genitalia of *S. praefica* clade female genitalia. 427, *S. praefica*. 428, *S. marima*. 429, *S. ornithogalli*. 430, *S. pulchella*. 431, *S. roseae*.

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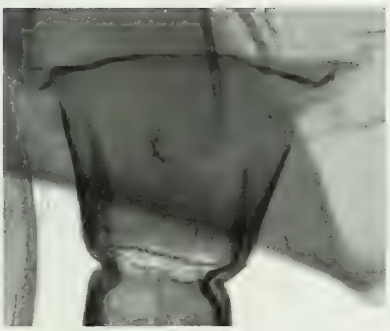

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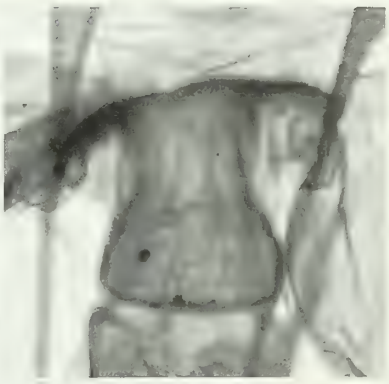

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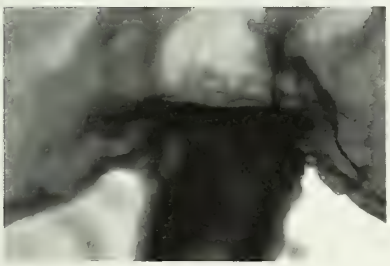

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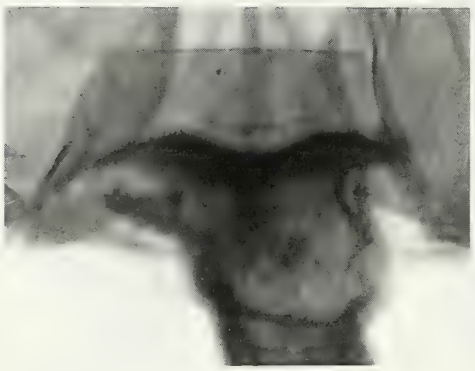
Figs. 432–437. Female ventral plate of ostium bursa of outgroups and *S. exigua* and *S. cilium* clade. 432, *Elaphria grata*. 433, *Galgula partita*. 434, *S. exigua*. 435, *S. cilium*. 436, *S. depravata*. 437, *S. pecten*.



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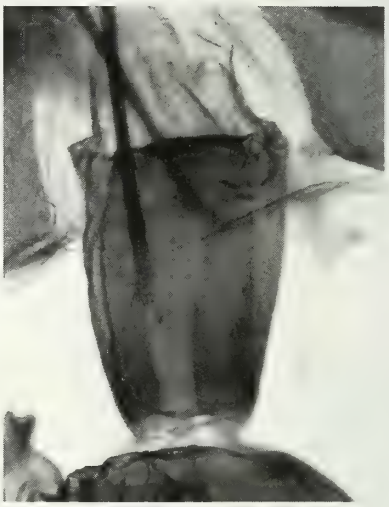

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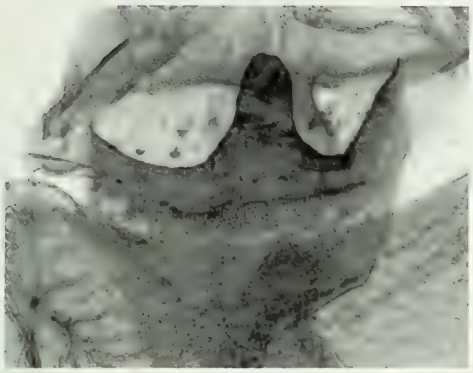
Figs. 438–441. *S. umbraculata* clade female ventral plate of ostium bursa. 438, *S. umbraculata*. 439, *S. pectinicornis*. 440, *S. apertura*. 441, *S. malagasy*.



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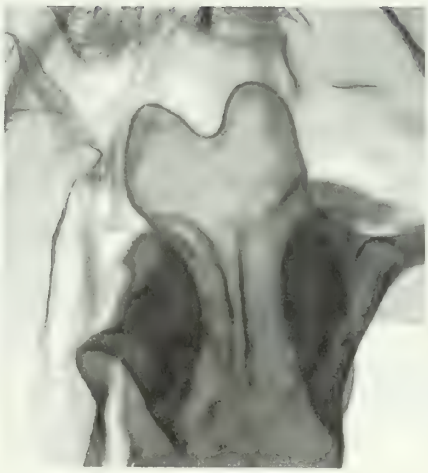

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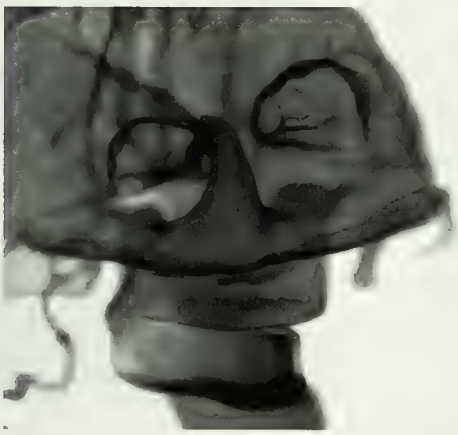

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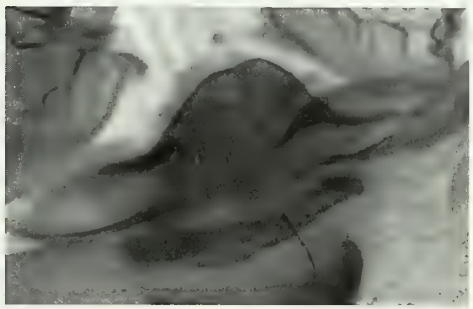

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Figs. 442–445. Clade 21 female ventral plate of ostium bursa. 442, *S. compta*. 443, *S. eridania*. 444, *S. albula*. 445, *S. ochrea*.

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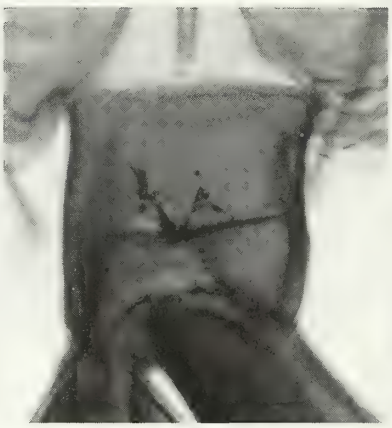

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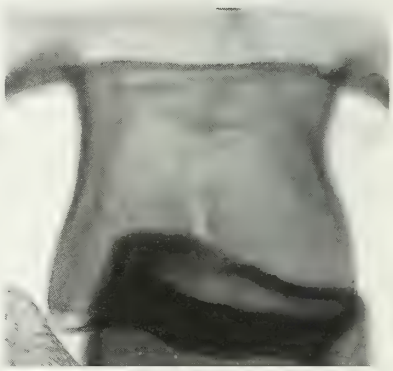

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Figs. 446–451. *S. exempta* clade, *S. frugiperda,* and *S. dolichos* clade female ventral plate of ostium bursa. 446, *S. exempta.* 447, *S. mauritia.* 448, *S.triturata.* 449, *S. frugiperda.* 450, *S. dolichos.* 451, *S. androgea.*

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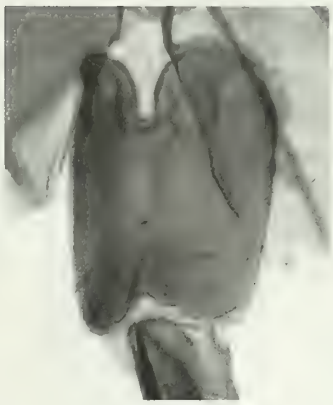

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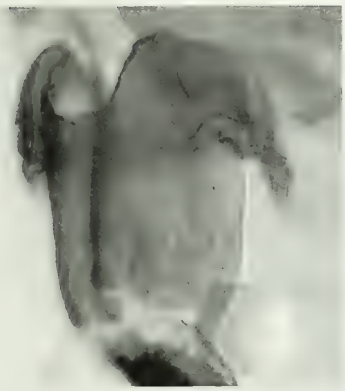

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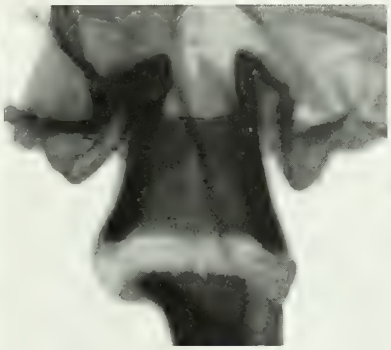

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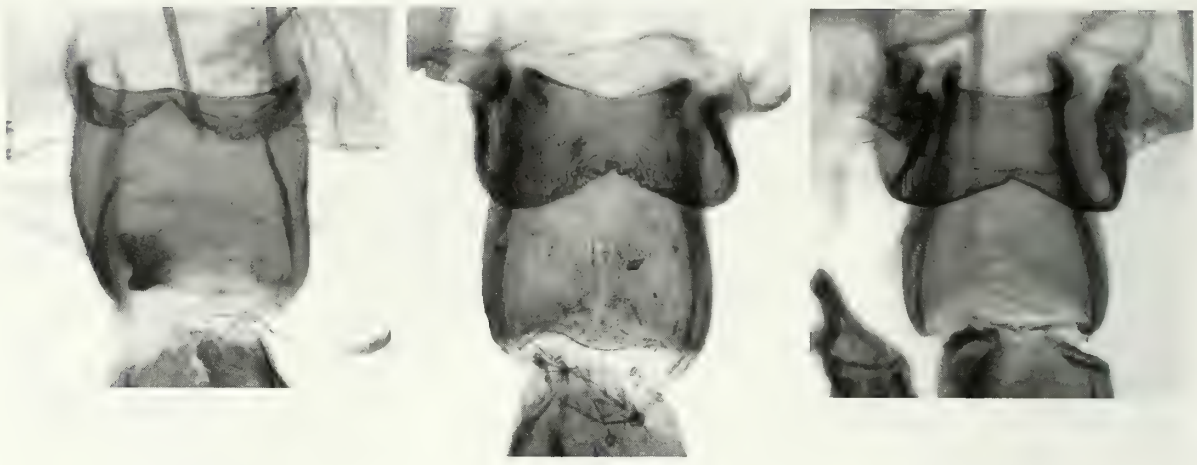
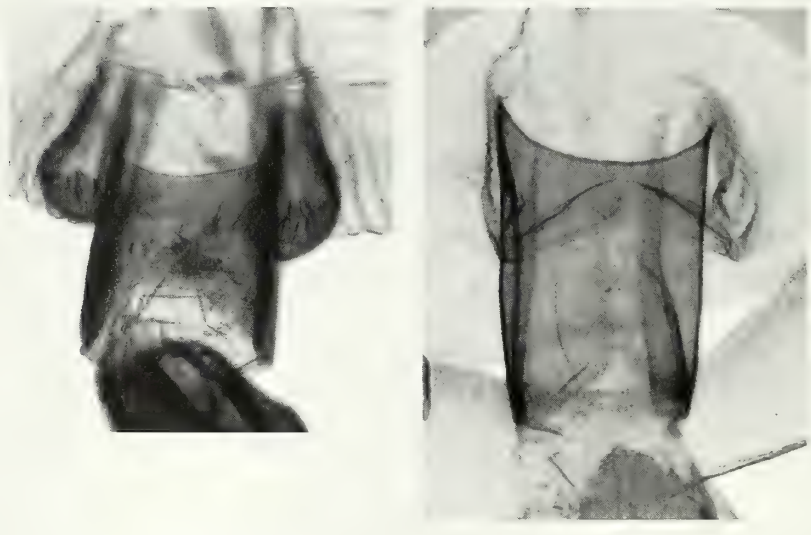
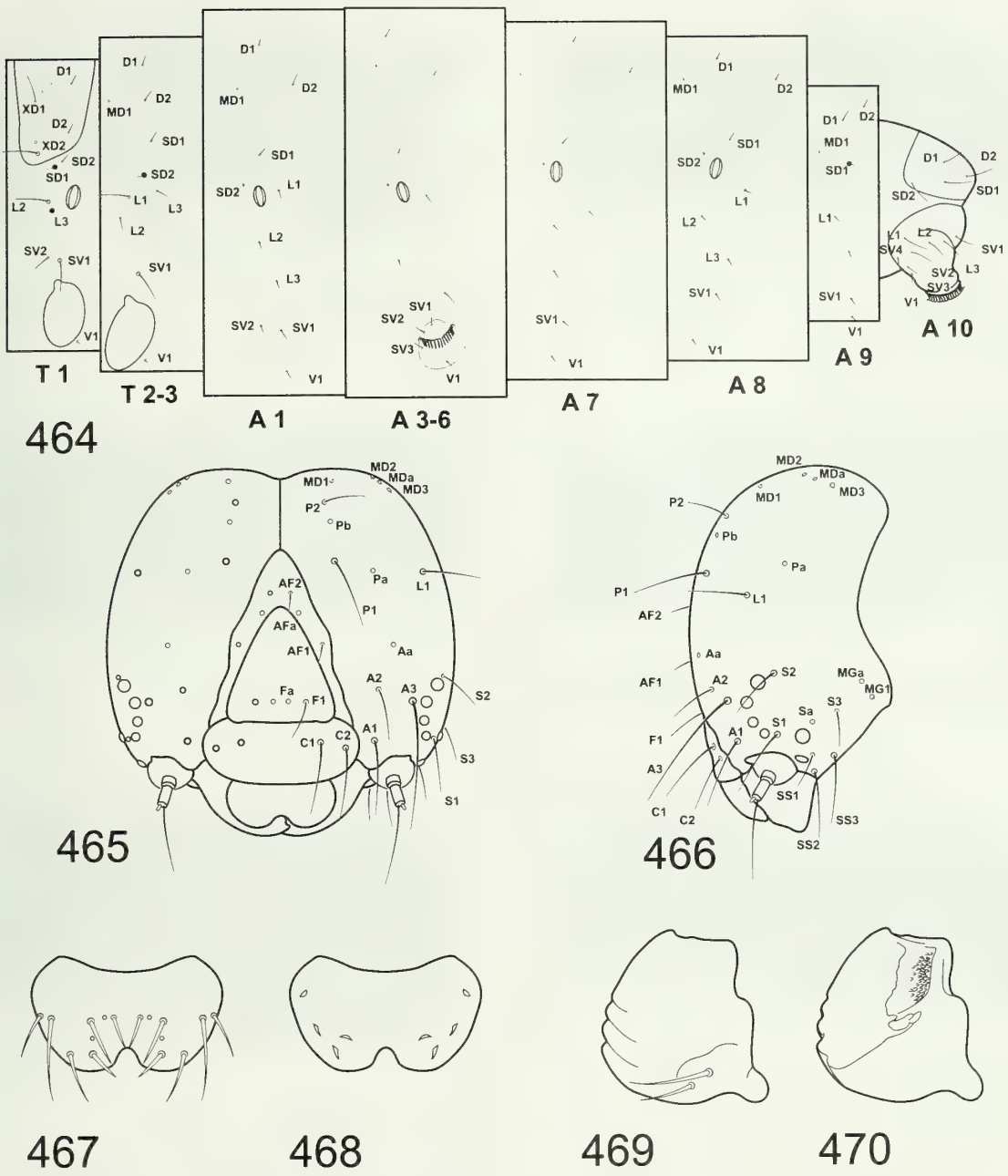
Figs. 452–458. *S. littoralis* and *S. evanida* clades female ventral plate of ostium bursa. 452, *S. littoralis.* 453, *S. litura.* 454, *S. picta.* 455, *S. evanida.* 456, *S. latifascia.* 457, *S. cosmiodes.* 458, *S. descoinsi.*

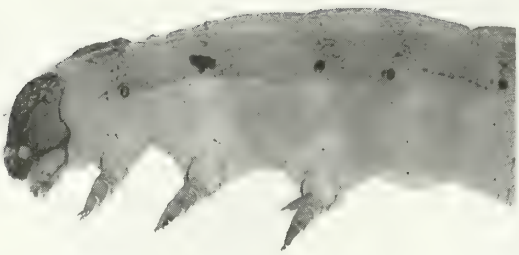




Figs. 459–463. *S. praefica* clade female ventral plate of ostium bursa. 459, *S. praefica*. 460, *S. marima*. 461, *S. ornithogalli*. 462, *S. pulchella*. 463, *S. roseae*.



Figs. 464–470. *S. mauritia* larva. 464, Setal map. 465, Head. 466, Head, lateral view (scale = 0.5 mm). 467, Labrum, dorsal view. 468, Labrum, ventral view. 469, Mandible, dorsal view. 470, Mandible, ventral view (scale = 0.1 mm).



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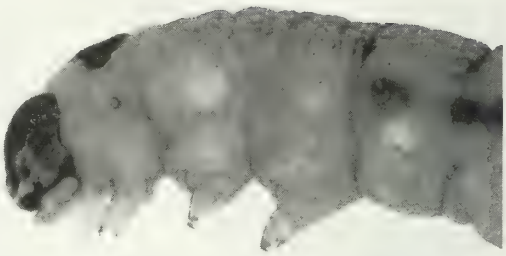

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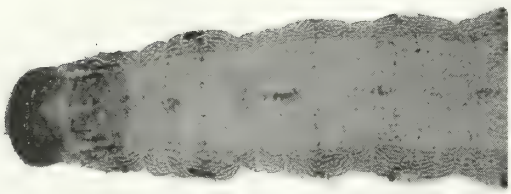

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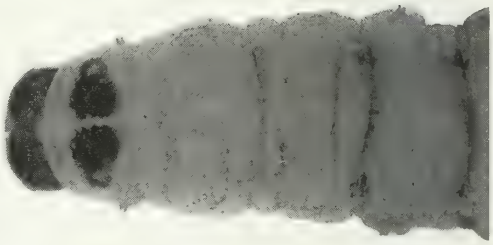

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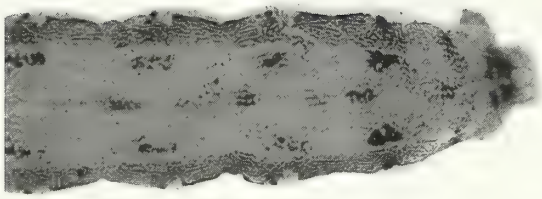

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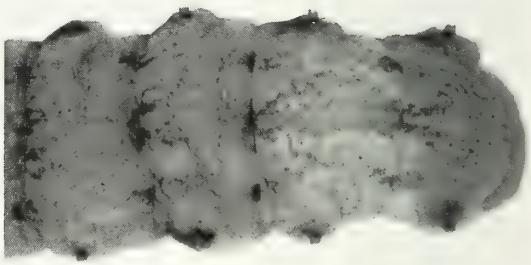

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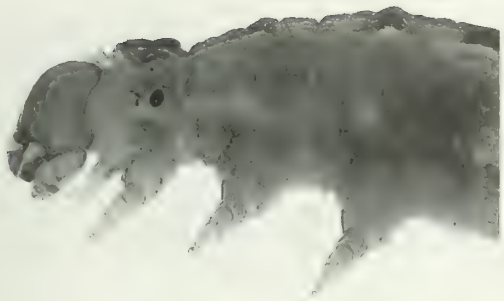
Figs. 471–476. *Spodoptera* larvae. 471, *S. exigua,* lateral view. 472, *S. exigua,* dorsal view. 473, *S. exigua,* dorsal view. 474, *S. pectinicornis,* lateral view. 475, *S. pectinicornis,* dorsal view. 476, *S. pectinicornis,* dorsal view.



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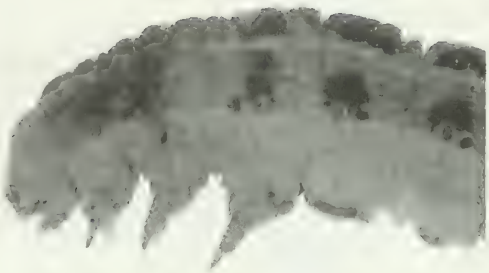

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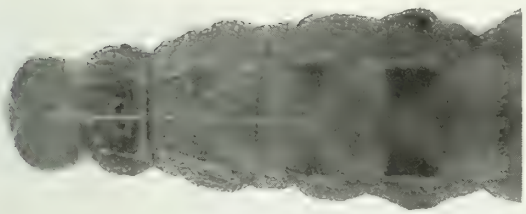

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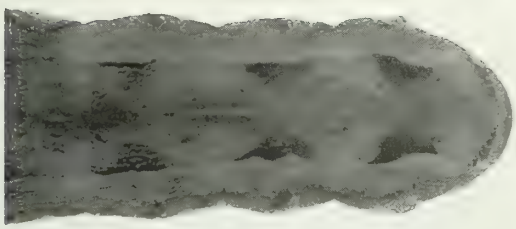

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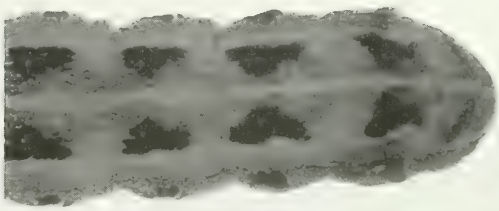

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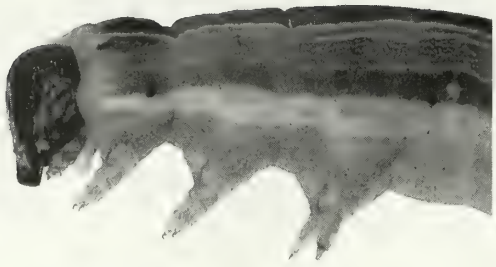
Figs. 477–482. *Spodoptera* larvae. 477, *S. eridania,* lateral view. 478, *S. eridania,* dorsal view. 479, *S. eridania,* dorsal view. 480, *S. albula,* lateral view. 481, *S. albula,* dorsal view. 482, *S. albula,* dorsal view.



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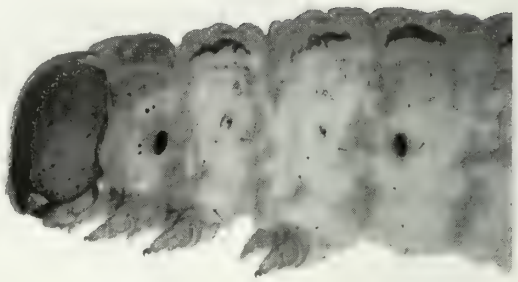

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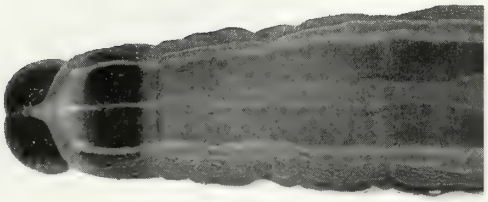

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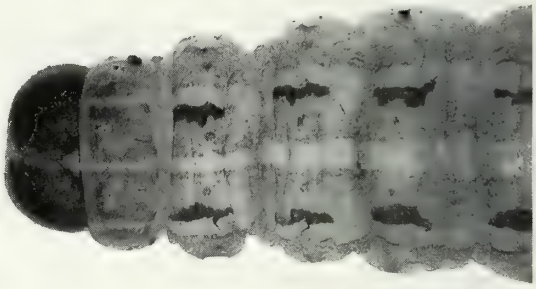

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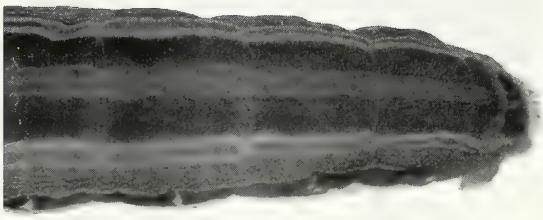

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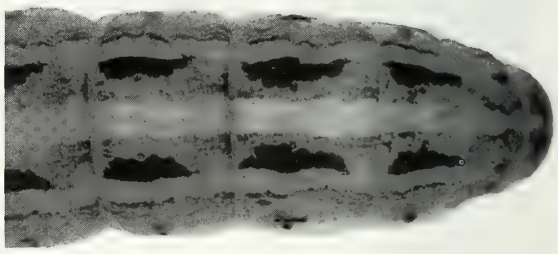

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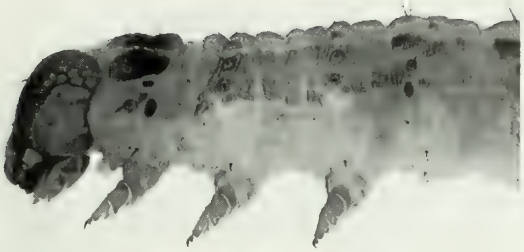
Figs. 483–488. *Spodoptera* larvae. 483, *S. exempta,* lateral view. 484, *S. exempta,* dorsal view. 485, *S. exempta,* dorsal view. 486, *S. mauritia,* lateral view. 487, *S. mauritia,* dorsal view. 488, *S. mauritia,* dorsal view.



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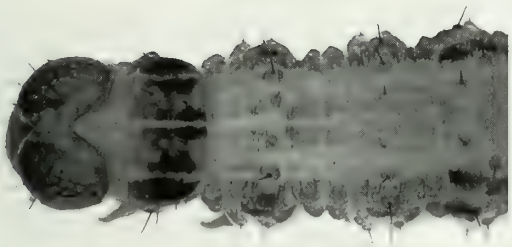

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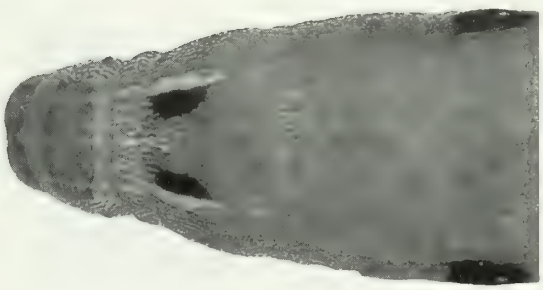

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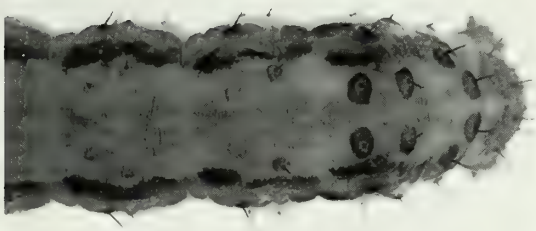

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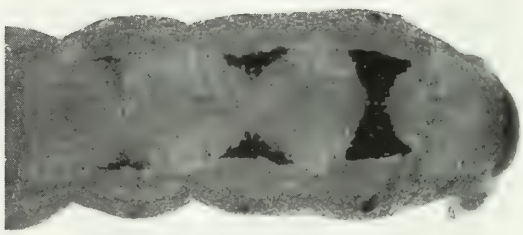

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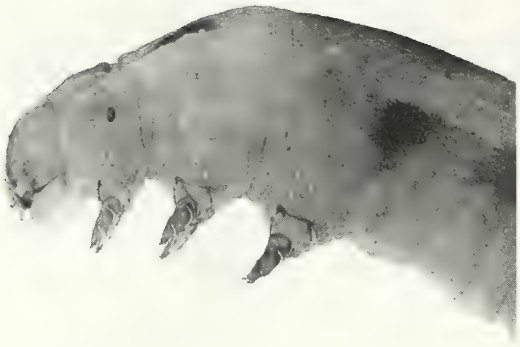
Figs. 489–494. *Spodoptera* larvae. 489, *S. frugiperda,* lateral view. 490, *S. frugiperda,* dorsal view. 491, *S. frugiperda,* dorsal view. 492, *S. dolichos,* lateral view. 493, *S. dolichos,* dorsal view. 494, *S. dolichos,* dorsal view.



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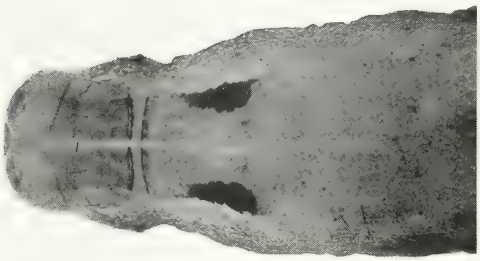

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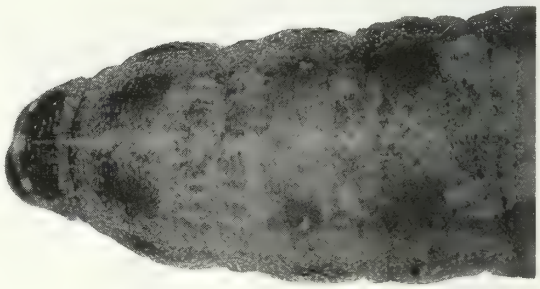

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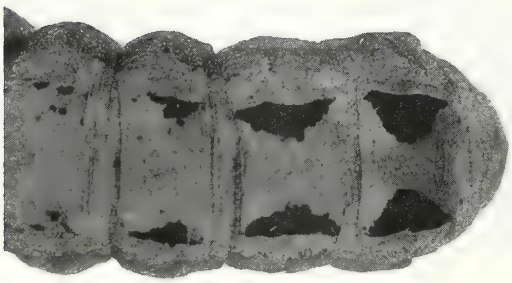

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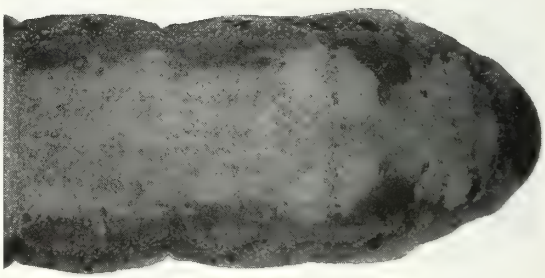

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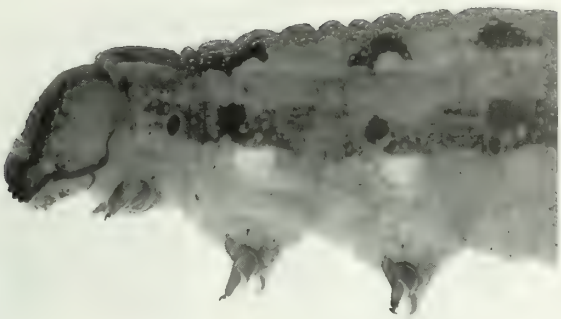
Figs. 495–500. *Spodoptera* larvae. 495, *S. androgea,* lateral view. 496, *S. androgea,* dorsal view. 497, *S. androgea,* dorsal view. 498, *S. littoralis,* lateral view. 499, *S. littoralis,* dorsal view. 500, *S. littoralis,* dorsal view.



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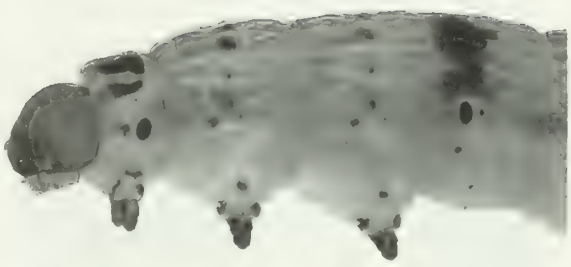

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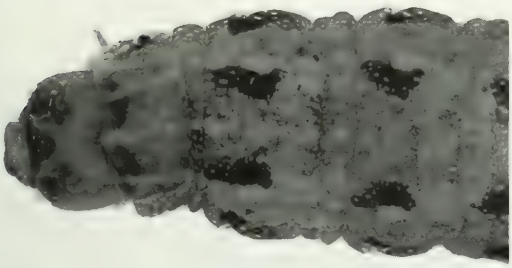

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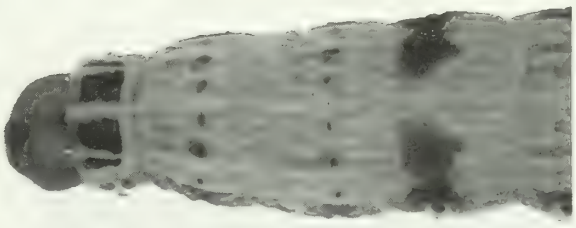

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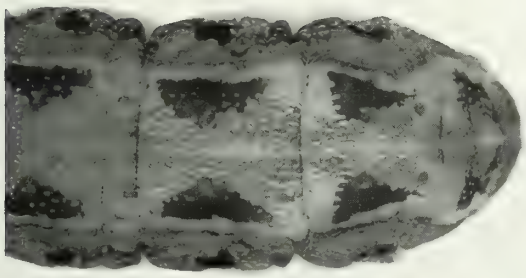

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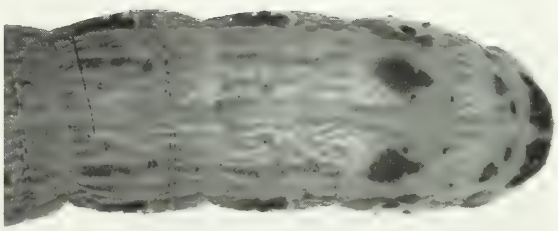

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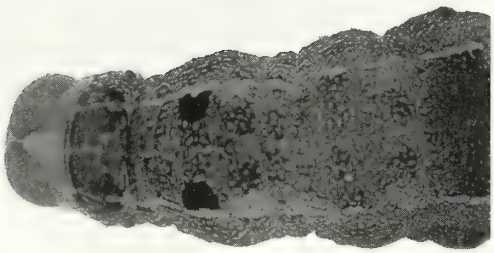

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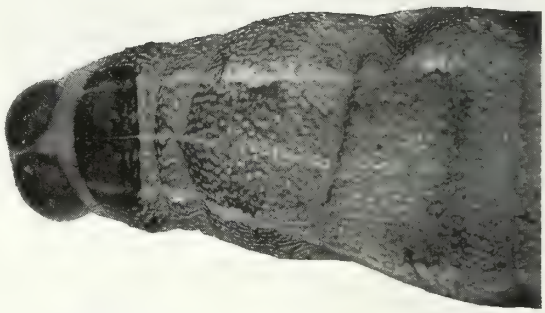

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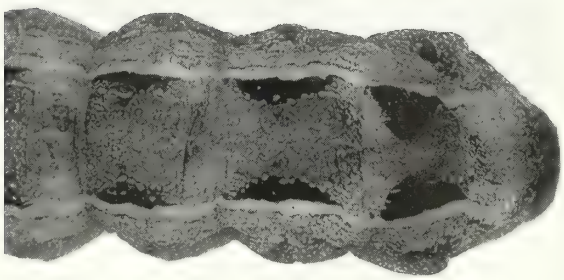

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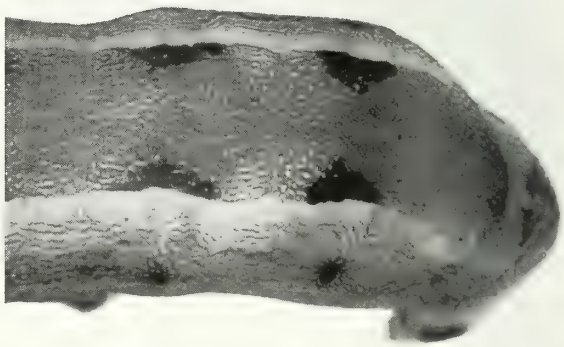

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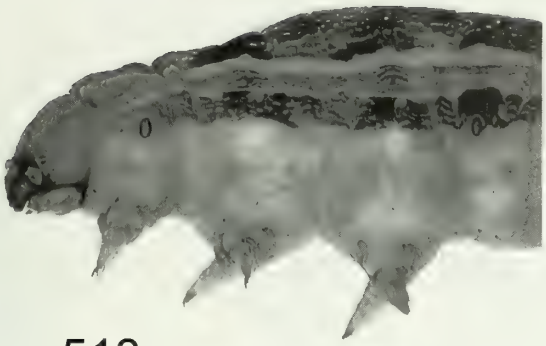

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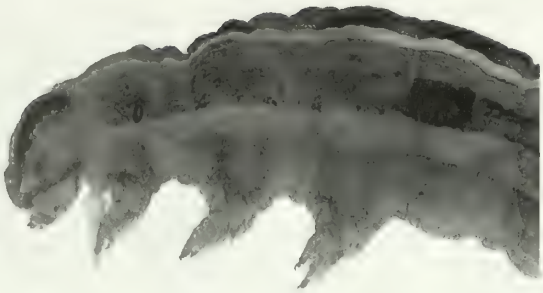

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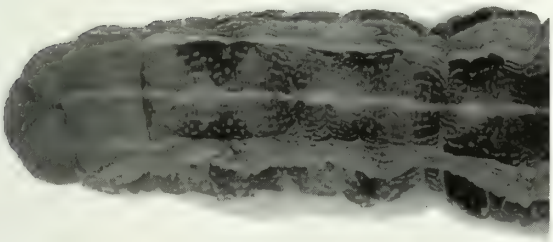

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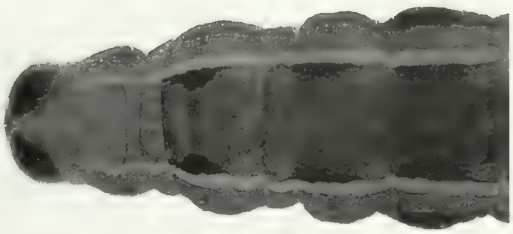

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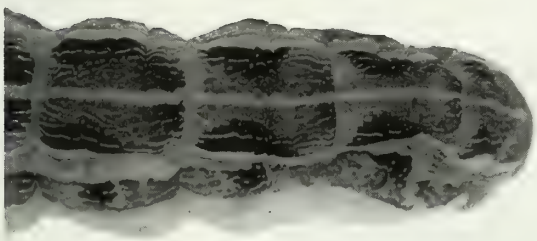

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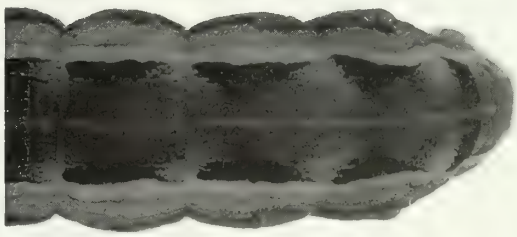

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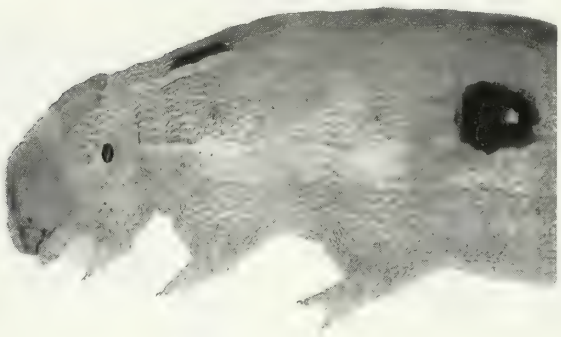

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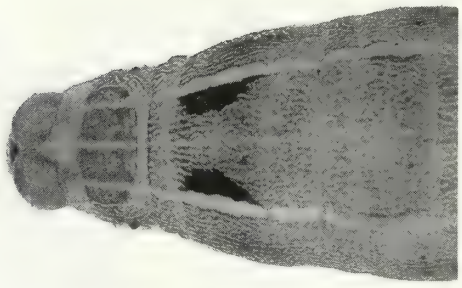

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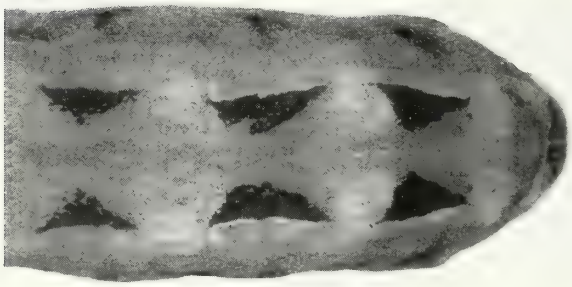

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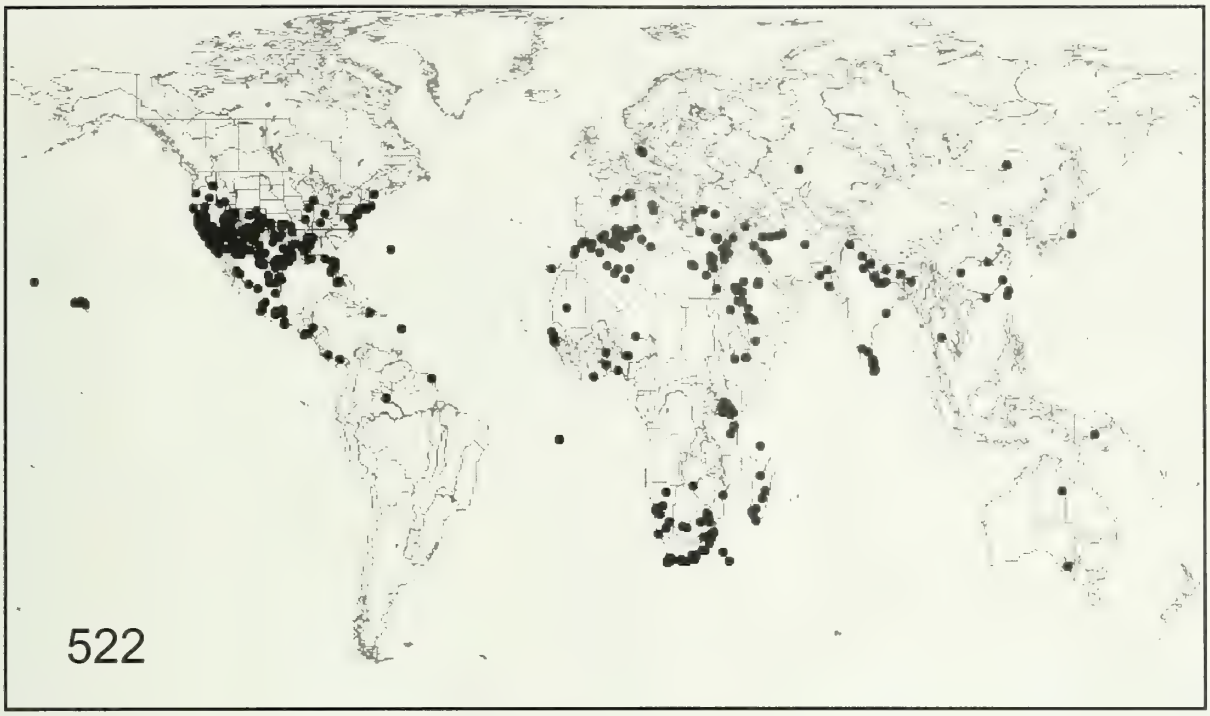

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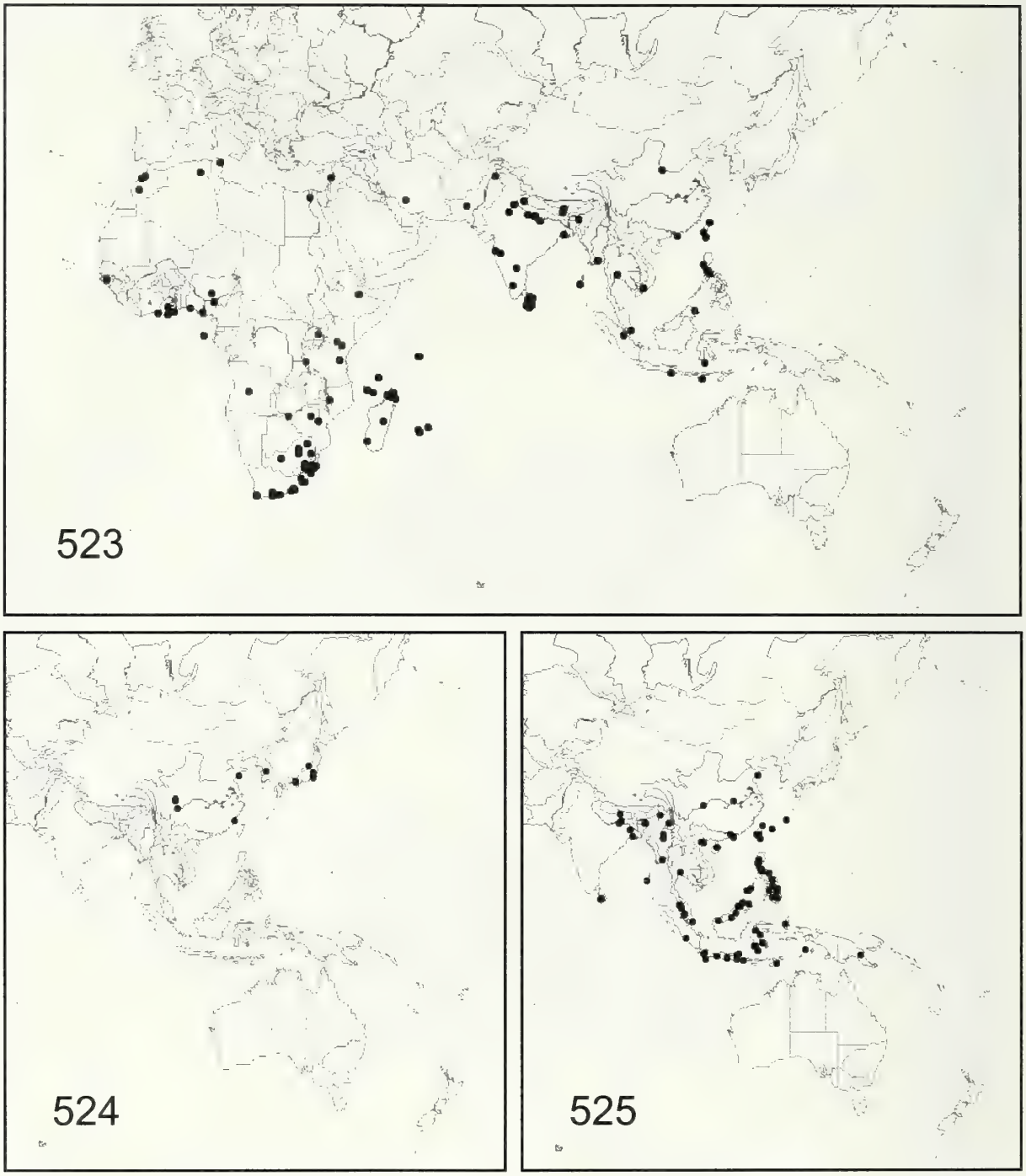

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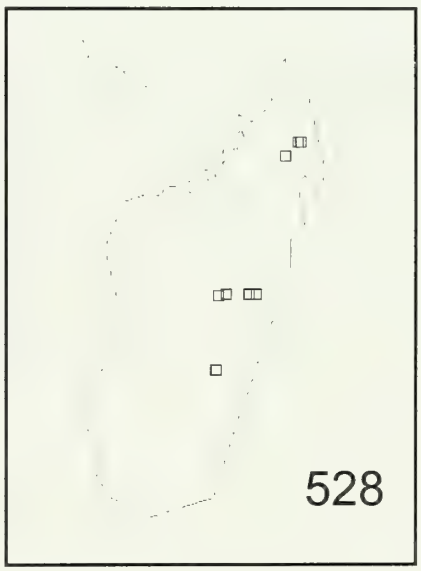

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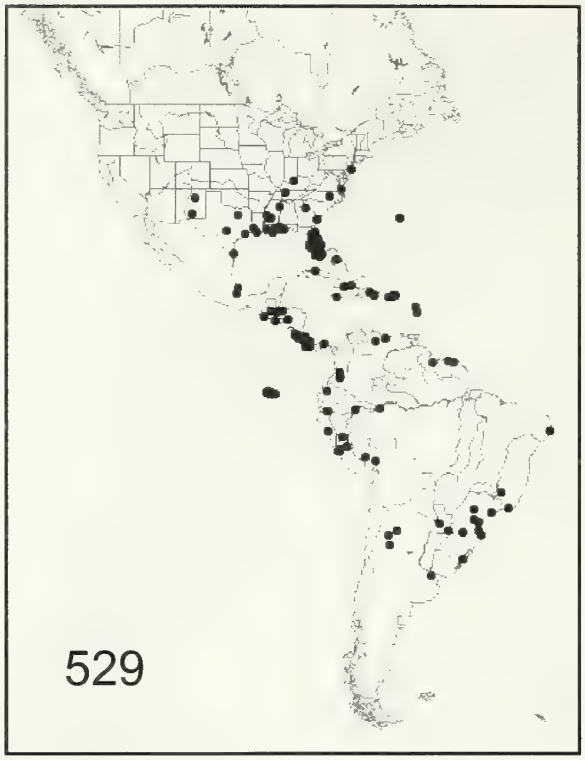

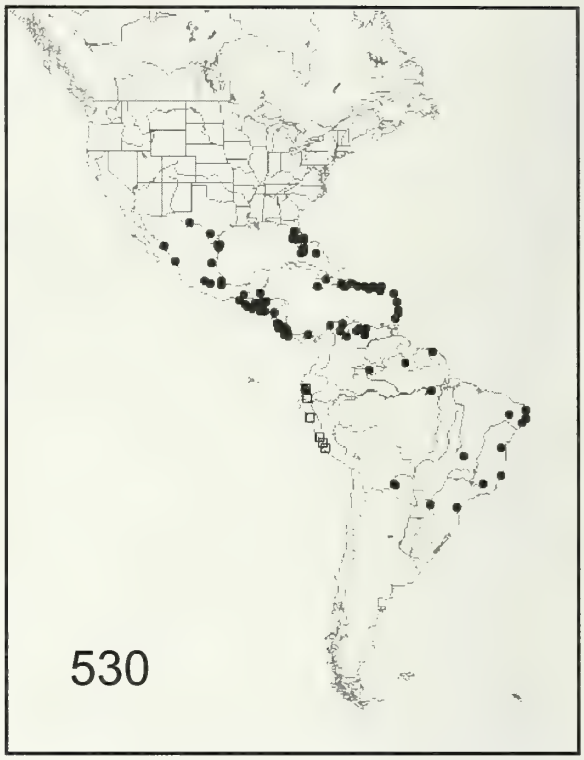

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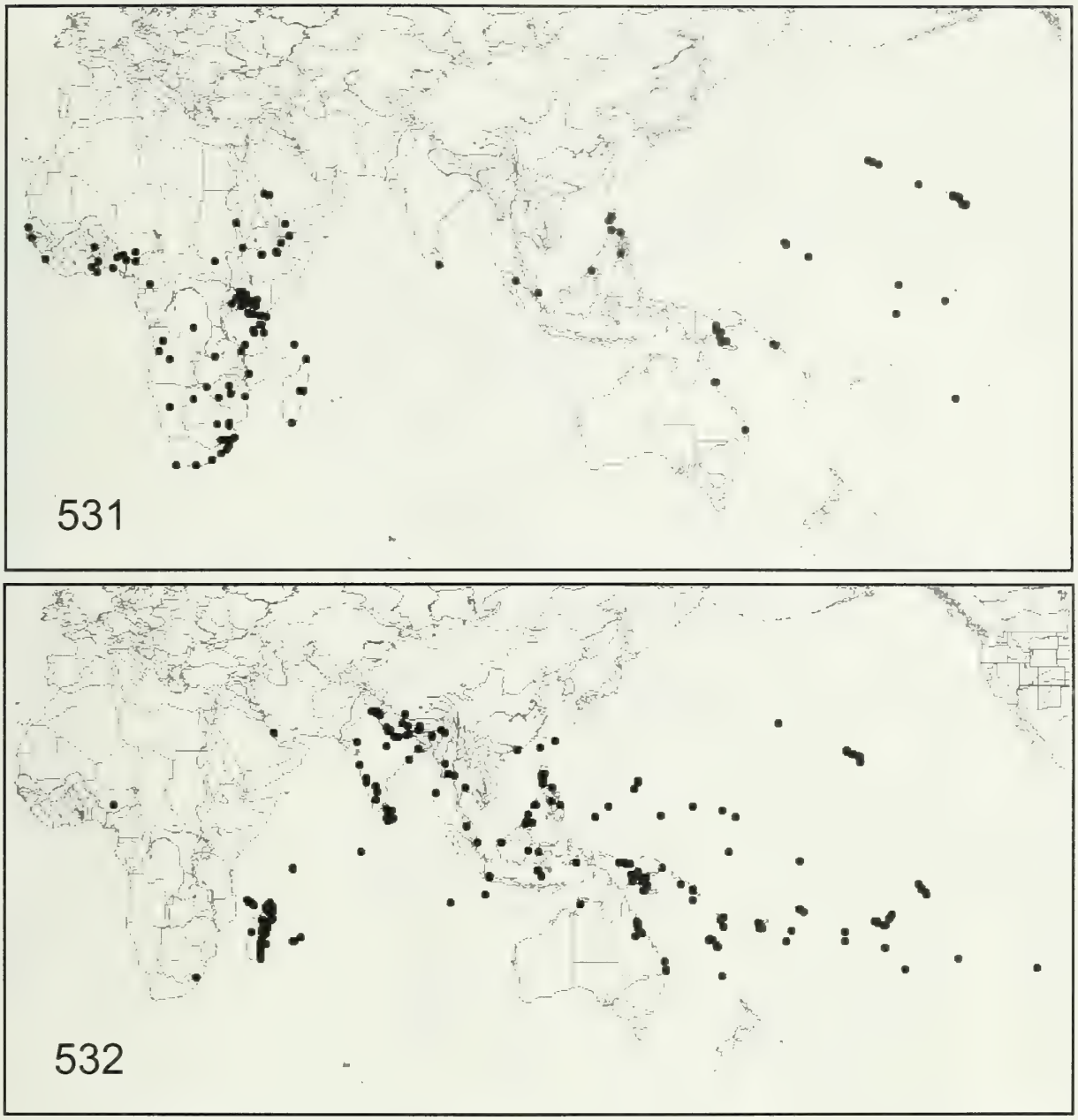

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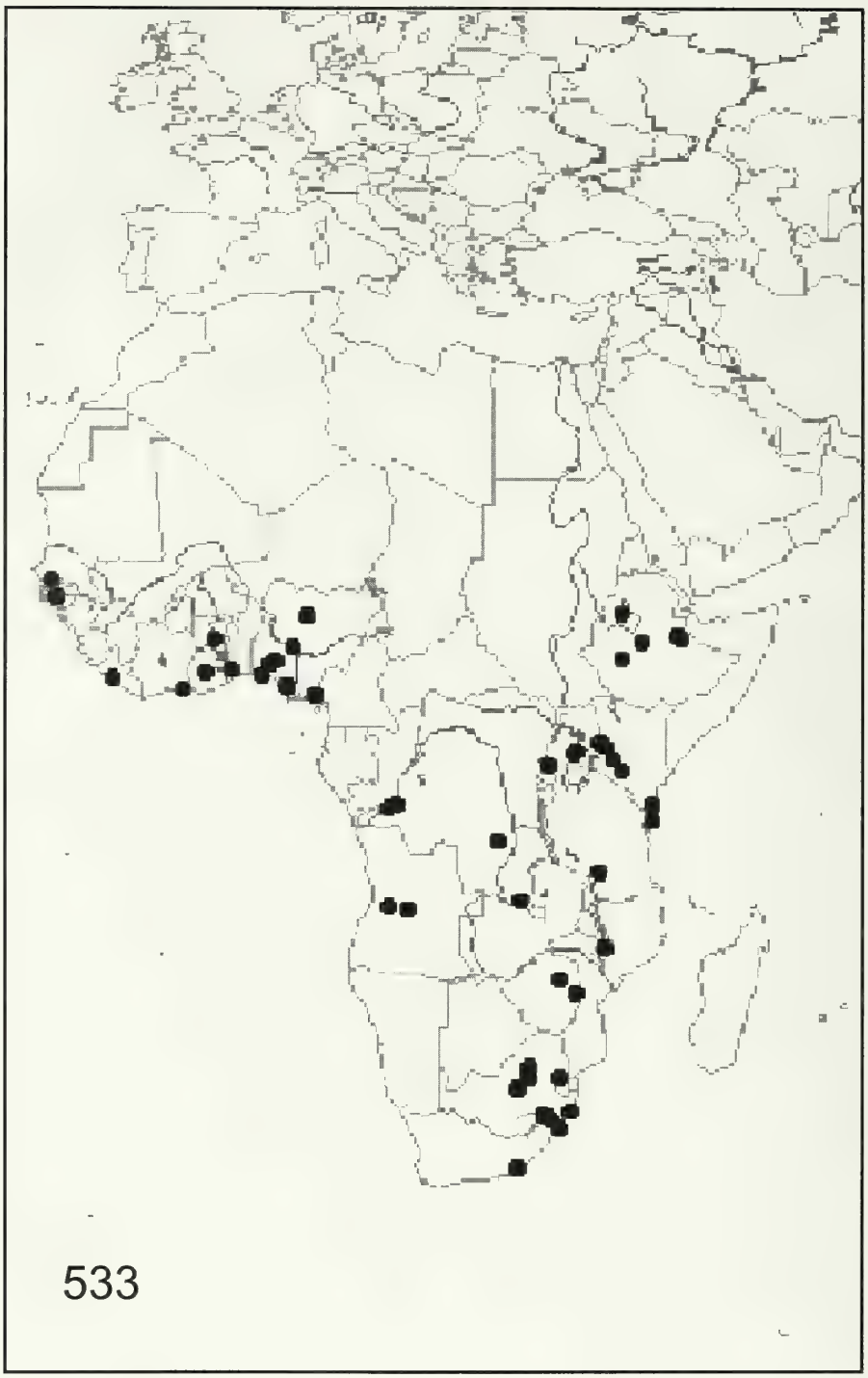

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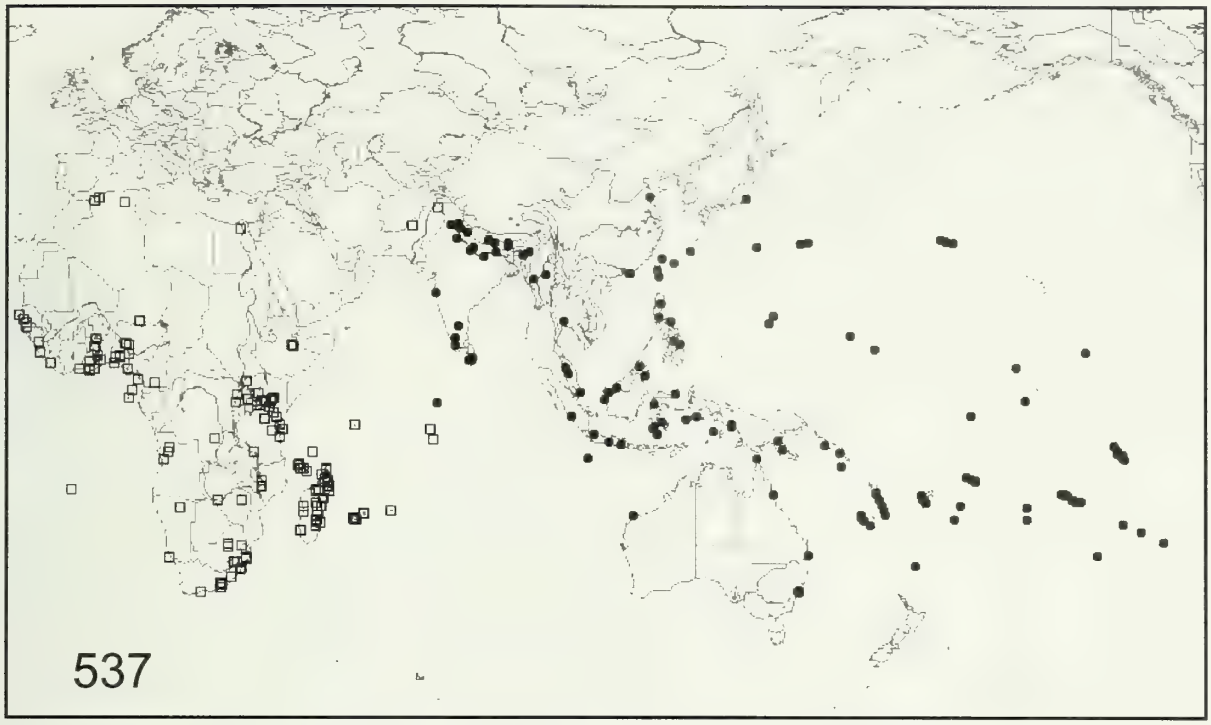

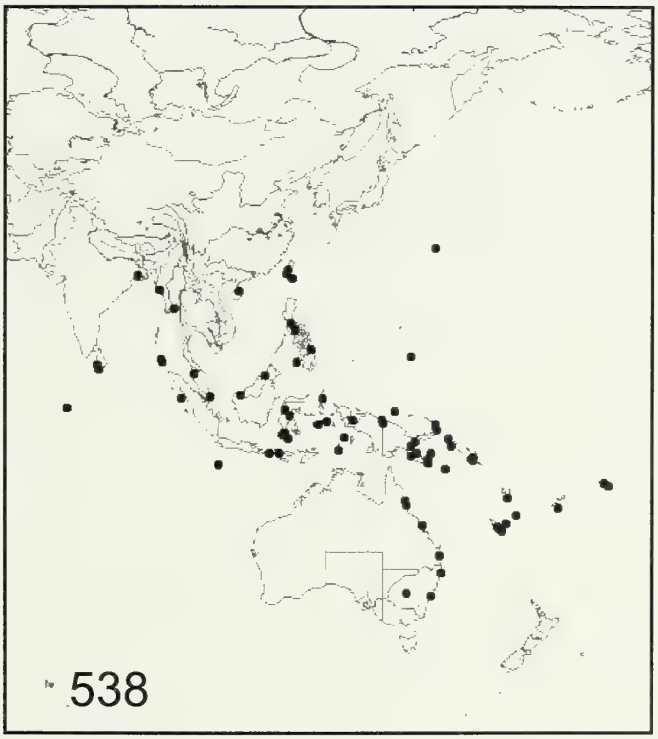

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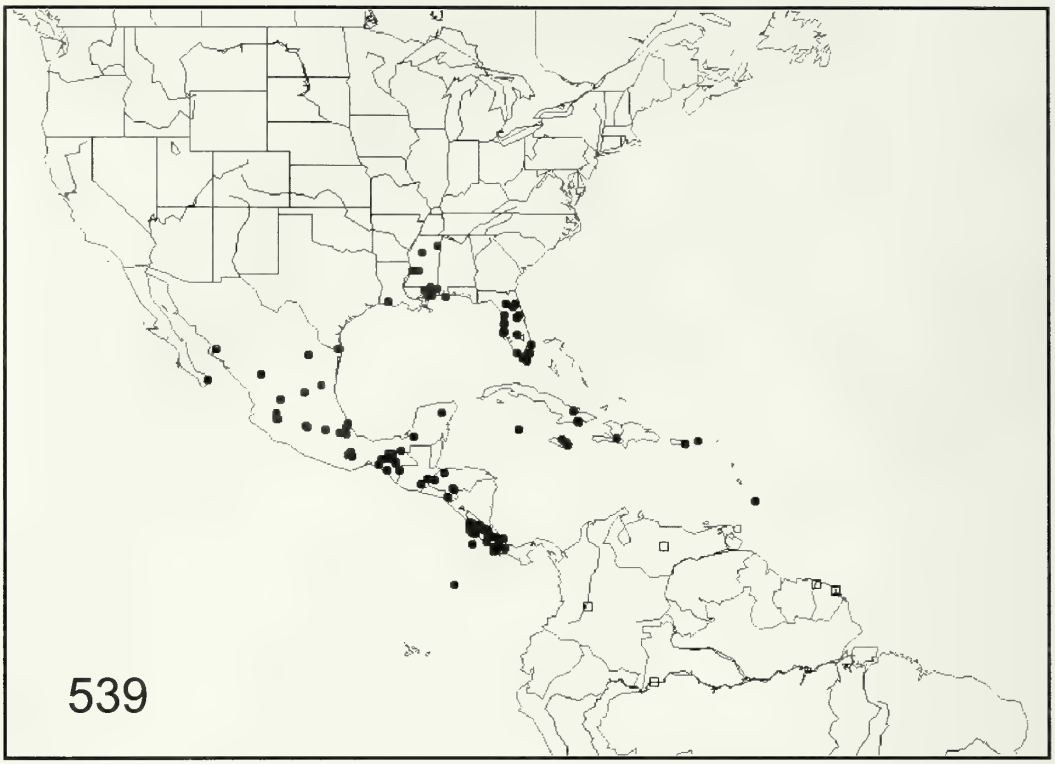

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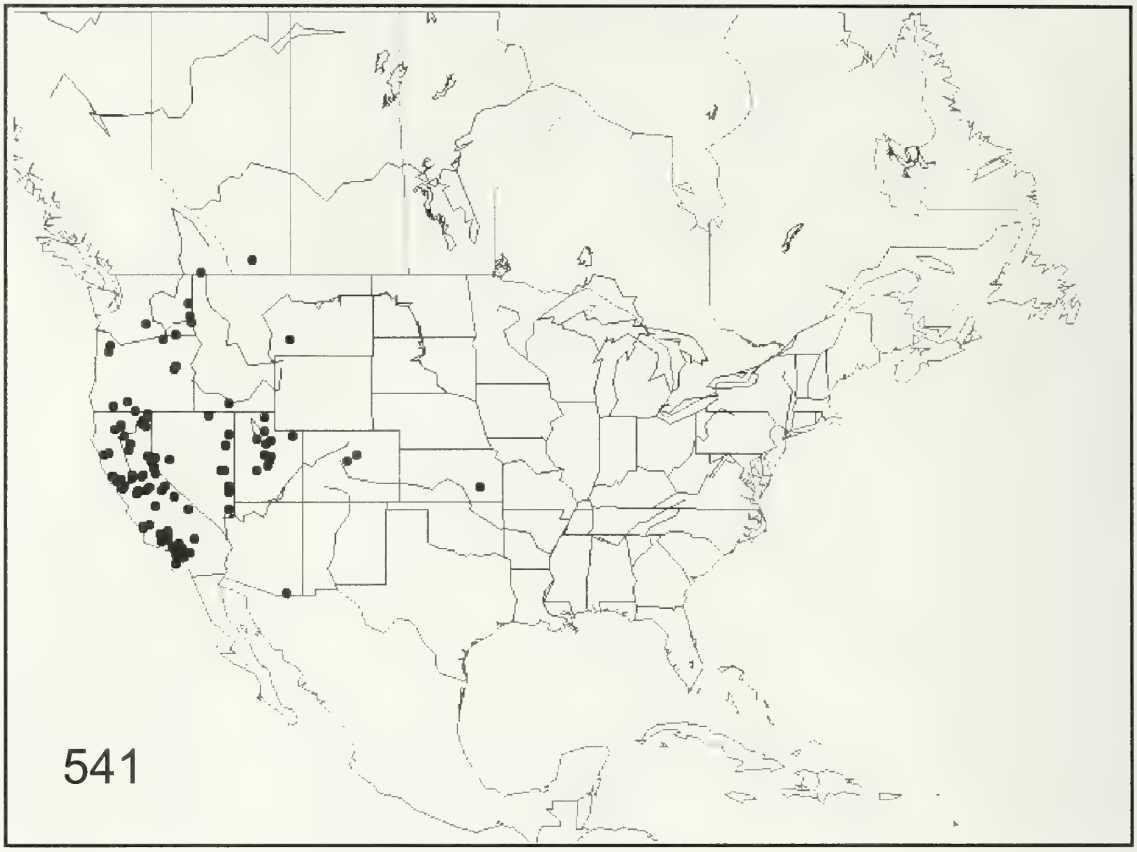

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